EFFECT OF MOISTURE STRESS ON PHOTOSYNTHESIS AND RESPIRATION IN MATURE LOBLOLLY PINE (*Pinus taeda* L.)

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CHAPTER I

INTRODUCTION

Loblolly pine has a natural range in the southeastern part of the United States covering about twelve states. The Atlantic coastal states represent the eastern edge and the natural range in the southeastern part of Oklahoma represents the western edge. Loblolly pine is the principal commercial pine species in the southeastern part of the United States due to its wide range, occurrence in pure stands, high productivity and its many uses in the paper, pulp and lumber industry. It is of prime economic importance to this region of the United States (Fowells 1965).

The biomass of a stand is the end product of the processes of carbon uptake, carbon allocation and carbon loss over the life of the stand. Tree productivity is to a large extent determined by the rate and efficiency with which the tree is able to conduct photosynthesis. The photosynthetic productivity of a tree is strongly influenced by factors of the environment. For example, photosynthetic tissues may experience wide variations in moisture content which affect the rate and integrity of many component reactions of photosynthesis. The

availability of essential resources for photosynthesis (light, water, carbon dioxide, and nutrients) also varies with time and habitat. Environmental stresses such as those imposed by drought, salinity, nutrient deficiency, pollutants, or excessively high or low temperatures have direct effects upon photosynthetic capacity (Govindjee 1982).

It is important to understand the growth characteristics of a tree because the productivity of a stand is determined by the tree's genetic potential, physiological processes, and its environment. Genetic and environmental factors control growth through physiological processes. Some of the important physiological processes which influence productivity are foliage photosynthetic and respiration rates and dry matter allocation. Some of the important environmental factors which influence productivity are moisture content of the soil, light intensity and carbon dioxide content, air temperature, and vapor pressure of the atmosphere.

Net carbon gain of a tree is a function of the rate of photosynthesis per unit of foliage, the respiration rate of the photosynthetic tissue, leaf area, and the surface area and respiration rate of non-photosynthetic tissue. These components can be related by the following formula:

$$\text{Carbon gain} = {}^{n}\Sigma_{i=1}\, L_i\, (A_i - R_i) - B_x\, (R_x)$$

where L_i is the leaf area of an age class foliage, A_i and R_i are the photosynthetic rate and respiration rate of that

age class, respectively, B_x is the surface area of non-photosynthetic tissue of type x (eg., root, stem, branch) and R_x is the respiration rate of that tissue (Teskey et al. 1987).

Biological stress is any change in environmental conditions that might reduce or adversely change a plant's growth or development (Levitt 1980). Stress of any kind affects the productivity of the stand. Water stress leads to a decrease in photosynthesis and respiration, injury to various cellular components, and altered patterns of assimilate allocation or carbon allocation. Water stress affects photosynthesis to a greater extent than respiration (Amthor, J.S. 1989), although respiratory loss was estimated to account for 58% of the total carbon fixed in loblolly pine (Kinerson 1975).

It has been shown that the photosynthetic response in loblolly pine varies with moisture stress levels (Seiler and Johnson 1985, 1988; Teskey et al. 1986, 1987). Moisture stress affects carbon allocation in loblolly pine (Boltz et al. 1986, Bongarten 1987). Photosynthetic response also varies with temperature and light levels (Teskey et al. 1986). Needles that develop in the lower levels of the canopy show morphological and physiological adaptation to the prevailing low light conditions. Their low photosynthetic capacity per unit leaf area may result from a low level of photosystem activity per unit leaf area (Lewandowska et al. 1977). Sun species grown under low

light intensities often develop characteristics similar to those of the shade species such as decreased maximum rate of photosynthesis (A_{max}), decreased dark respiration (R_d), increased specific leaf area (SLA) and increased chlorophyll content (Bjorkman 1981). Chlorophyll content decreases under low light conditions (Oquist et al. 1982), but Higginbotham (1974) found that chlorophyll content did not vary between the upper and lower portions of a loblolly pine canopy.

Some of the previous observations have been based on results obtained from experiments on seedlings. But it is very important to understand the effect of moisture stress on photosynthesis and respiration in mature trees, since it helps in understanding how these factors affect productivity in mature stands.

The phenomenon of global warming, or the "greenhouse effect", is one of the most important issues being debated in recent times. There has been an elevation in the concentration of carbon dioxide and other trace gases since the industrial revolution, largely as a result of man's activities which have increased the radiative heating of the troposphere. The effects of a potential future climate described by elevated carbon dioxide, reduced precipitation and increased temperature on tree and forest stand growth are uncertain.

Fluxes of carbon dioxide and water vapor from forests are major components that must be quantified if reliable

models are to be constructed to predict the effects of increased carbon dioxide, temperature, precipitation, and water vapor regimes on global climate and forest health and productivity. Tans et al. (1990) have recently provided evidence that the role of terrestrial ecosystems as a sink for carbon dioxide may have been greatly underestimated in the global circulation models. Therefore, quantifying the magnitude of the flux from highly productive temperate forest ecosystem is important to understand the interaction between forests and carbon dioxide levels in the atmosphere. In addition, water availability, temperature and the concentration of carbon dioxide are critical factors affecting forest health and productivity. In order to assess the effect of these potential changes on our timber and water resources we must be able to predict how forest carbon exchange and water use will respond to altered carbon dioxide, temperature, precipitation and water vapor regimes.

The objective of this research was to:

Quantify the effects of moisture stress on diurnal and seasonal changes in photosynthesis, foliar respiration, and stomatal conductance in mature loblolly pine.

The important hypotheses for this study were

a) Annual net carbon gain is predominantly limited by stomatal closure due to high evaporative demand and low soil moisture over extended periods.

b) High respiration rates due to extended periods of elevated temperature reduce net primary productivity.

c) Shading decreases net carbon gain and stomatal conductance in approximate proportion to the level of shade at each canopy position in both irrigated and non-irrigated trees.

CHAPTER II

MATERIALS AND METHODS

Site Description

The study site is a 19-year old loblolly pine plantation situated on Weyerhaeuser Company property in southeastern McCurtain county, approximately 8 km south of Eagletown, Oklahoma. Summers are hot and humid while the winters are usually mild. Average annual precipitation is 119 cm/year with the highest amount occurring in spring. The soil is a Cahaba fine sandy loam of the Guyton-Ochlockonee association. The soil is deep and has 0-1% slopes. The maximum soil water holding capacity of the top 1.2 m is 23.17 cm (USDA SCS, 1974).

The site was prepared by burning and double bedding after the harvest of a pine-hardwood stand in 1975. The stand was established from unimproved seed. At the beginning of the present study in July 1991, the mean basal area of the study portion of the stand was 22.52 m^2/ha in the irrigated plot and 24.49 m^2/ha in the non-irrigated plot and exhibited a site index of 19.3 m (base age, 25 years).

Study Design

Two 0.1 ha treatment plots were compared in the study, each nested within a 0.04 ha measurement plot. In one plot, the soil moisture tension was measured by eight porous cup soil tensiometers located at a depth of 15 cm. The plot was watered through a sprinkler system network when the average soil tensiometer readings fell below -0.05 MPa. The other plot was non-irrigated and served as control. Vegetation was controlled in the irrigated plot by annual spraying of glyphosate (Roundup) herbicide to conserve soil moisture by limiting transpiration of the under-growth.

Environmental Variables

Values of daily air temperature, precipitation, relative humidity, vapor pressure deficit, and pan evaporation for the region were obtained from the National Oceanic and Atmospheric Administration records from the United States Army Corps of Engineers' weather station at Broken Bow Dam, Oklahoma, approximately 27 km from the study site. On-site precipitation was measured with two standard rain gauges situated at two open areas adjacent to the plots. The daily temperature, relative humidity and wind speed data were obtained from the weather station on site. The carbon dioxide exchange system measured the instantaneous photosynthetically active radiation, air temperature, and relative humidity for a set of needles.

Net Carbon Exchange

Net photosynthesis and respiration was measured on three selected trees per plot using a closed-flow carbon dioxide exchange system (LiCor 6200 Portable Photosynthesis System, Lincoln, NB). This system consists of an infra-red gas analyzer which determines the amount of carbon dioxide content in the air being sampled, a computer controlled console which stores the data collected, a quarter liter leaf chamber which houses the needles during the measurement and a set of batteries which powers the whole system. The IRGA operates on the principal that carbon dioxide absorbs infra-red radiation. This system can measure photosynthesis, respiration, stomatal conductance, transpiration, light intensity (PAR), air temperature, relative humidity and carbon dioxide concentration. The quantum sensor, located outside the leaf chamber, measures the photosynthetically active radiation.

Prior to each operation the instrument was calibrated by using a known concentration of carbon dioxide gas. The known carbon dioxide concentration was measured and the zero and span on the analyzer were adjusted until the readings were correct. The instrument was turned on for about 15-20 minutes with the pump on. The instrument was then connected to the tank of known concentration. The flow was set to around 1000 μmol s^{-1} and carbon dioxide concentration was monitored. The carbon dioxide scrub was turned on and zero was set. Then the scrub was turned off

and span was set. This was done until the readings were consistent. During this whole process the pump was turned off.

Fifteen needles (5 fascicles), each with a length of at least 6.5 cm, were enclosed in the leaf chamber and the average rate of change in carbon dioxide concentration in the air was determined for a short period of time (30 seconds). The photosynthetic and respiration rate was then calculated internally using the rate of change in carbon dioxide concentration plus the amount of needle surface area enclosed in the chamber, air temperature, vapor pressure deficit, and other factors. An equation was used to determine the needle surface area:

$$A(cm^2) = 2RFL\ (N + \pi)$$

where R is the average radius of the fascicles, F is the number of fascicles, L is the total fascicle or average fascicle length, and N is the number of needles per fascicle. The radius was measured using a magnifying glass (Bingham 1983).

Two crews of three persons per plot were required during the carbon dioxide measurement. On each plot, one person operated a LiCor 6200, the other person placed the needles in the cuvette, and the third person measured needle water potential.

The observations were obtained at three different crown positions: upper one-third, middle one-third, and lower one-third of the crown. Access into each tree crown

was provided by a 20.0 m high, 0.32 m wide tripod base T.V. tower with three 1.83 m long swingable platforms attached at the appropriate measurement levels. The observations were taken on the mature needles of the second flush of the previous year (1990) and on the current year flush. During each measurement day, pre-dawn needle water potential was measured with a Scholander-type pressure bomb to the nearest 0.01 MPa. The carbon dioxide exchange measurements were obtained four times a day starting with a pre-dawn respiration measurement, and then at intervals of three hours starting from 8:00 a.m till 5:00 p.m. After every carbon dioxide exchange measurement the needle water potential was measured. The same "co-hort" of needles were used for measurements throughout the day.

Pines selected on the irrigated plot had an average height of 16.10 m, a basal area of 22.52 m^2/ha, and diameter at breast height of 29.00 cm and the pines selected on the non-irrigated plot had an average height of 17.00 m, a basal area of 24.49 m^2/ha, and diameter at breast height of 27.90 cm. The gas exchange observations were obtained on the needles located on the south side of the tree. The gas exchange observations were obtained during the months of July, August and October of 1991 and during the month of April 1992. Frequent precipitation in May, June, July, August and September in 1992 negated soil moisture differences between the irrigated and control plot, therefore measurements as originally planned were not

made during these months. The same complement of needles were used for measurement during the whole season. During the month of October the branch used for taking measurements in the lower one-third portion of the canopy on the irrigated plot abscised and hence it was necessary to move to next higher branch in the lower one-third portion of the canopy. During the month of April 1992, only the needles from the second flush of 1991 were used for measurement because the needles of the first flush of 1992 were not long enough to span the leaf chamber during measurement. Some of the needles used for obtaining observations at the top one-third portion of the canopy were different from the needles used in 1991 because some of the branches were damaged due to a wind storm and thunderstorm which occurred during the later part of March.

Respiration measurements were obtained by covering the leaf chamber with a black cloth and then allowing the needles to equilibrate to the conditions in the leaf chamber. The leaf chamber was shaded so that the temperature did not vary to a large extent in the leaf chamber during the period of measurement. The respiration rate was then calculated internally using the rate of change in carbon dioxide concentration plus the amount of needle surface area enclosed in the chamber, air temperature, vapor pressure deficit, and other factors.

The chlorophyll content was estimated using the Acetone method (Arnon 1949) after each measurement.

Analysis

The objective of this study was to quantify the effects of moisture stress on photosynthesis, respiration and stomatal conductance. The data was analyzed using the stepwise backward regression procedure (Leabo 1976). This technique uses a simple correlation matrix. A regression between the independent variable most highly correlated with the dependent variable is obtained. Then the partial coefficients generated with respect to the other variables are used to select the next variable that enters the model. Any independent variable found not significant in terms of improving the regression equation is rejected. This stepwise procedure is continued until all the independent variables are used up.

Stepwise regression selects one independent variable at a time (i.e, step by step) by calculating the optimum coefficients for a linear mathematical equation. The procedure minimizes the squared deviations of the predicted value of the dependent variable from the actual value of the dependent variable, which means that the best straight line is fitted to the data.

The relationships of photosynthesis and stomatal conductance to various environmental parameters and plant parameters were examined using the stepwise regression method. All the analyses were performed on a microcomputer using PC-SAS (SAS Institute Inc. Cary, NC). Independent variables like crown position, age-flush class and

irrigation were represented by dummy variables. In the model DV1position means that the upper crown position is being compared to the lower crown position and DV2position means that the middle crown position is being compared to the lower crown position. In the model DVflush is equal to 1 if the flush is from 1991 and DVflush is equal to 0 if the flush is from 1990. In the model DVirrigation is equal to 1 if the plot is irrigated and DVirrigation is equal to 0 if the plot is non-irrigated. The regression models of photosynthesis and stomatal conductance were developed for each month using the independent variables such as quantum, total chlorophyll, xylem pressure potential (water potential), air temperature, vapor pressure deficit, humidity and the dummy variables which represent crown position, age-flush class and irrigation. Regression models of photosynthesis and stomatal conductance were developed for the whole season using the independent variables listed above. All the variables in the model were considered to be significant at P=0.10 level.

The aim of this study was to determine if irrigation affected the carbon exchange rate and stomatal conductance and to identify the most important variables that affected these two physiological processes and to describe how they are related. The analysis was done for each month and also for the whole season. During the development of the regression models of photosynthesis and stomatal conductance for the whole season the month of October was

used as the month to which the other months were compared. This was done because in the month of October the treatment differences between irrigated and non-irrigated plots were most clearly expressed.

CHAPTER III

RESULTS AND DISCUSSION

Environment

The amount of precipitation received in the months of April and May of 1991 was 8.85 cm and 13.62 cm greater than the monthly average recieved in the region (fig. 1). Average monthly precipitation was based on the data recorded from 1951-1980 at Idabel. In the study period pan evaporation exceeded precipitation during the months of June, July, August, and September in 1991 (fig. 2). In 1992 the amount of precipitation received in summer was similar to the monthly average, but later on in the year the amount of precipitation received was greater than the monthly average (fig. 1). In 1992 precipitation exceeded pan evaporation in January, February, March, and April (fig. 2).

Xylem Pressure Potential

The xylem pressure potential decreased diurnally from a higher pre-dawn value to a lower value in the middle of the day (fig. 3-6). The xylem pressure potentials were obtained on only one flush i.e, either the 1990 or 1991 flush. This was because in a previous study it was

concluded that xylem pressure potential did not differ between flushes. In the month of April 1992 pre-dawn xylem pressure potential could not be obtained in the middle and upper crown positions due to the formation of dew on the needles (fig. 6). The pattern of xylem pressure potential obtained in August 1991 was not similar to the one obtained in the other months because of cloudiness on the measurement day. Hence the lowest values of xylem pressure potential were obtained only at the end of the day instead of being obtained in the middle of the day (fig. 4).

The daily pattern of xylem pressure was similar in both the irrigated and non-irrigated plots but the xylem pressure was slightly more negative in the non-irrigated plot. The daily pattern of xylem pressure potential is similar to that observed in other species of conifers (Hellkvist 1974, Leverenz 1981, Beadle et al. 1985a, Teskey et al. 1984). A similar pattern of xylem pressure potential has also been observed in loblolly pine seedlings (Fites and Teskey 1988).

Pre-dawn xylem pressure potential is a very good indicator of the amount of moisture in the soil. The figures 3-6 depict the xylem pressure potential in both the irrigated and non-irrigated plots. The lowest mean pre-dawn water potential value recorded for the irrigated plot was -0.56 MPa in October 1991 and the lowest mean pre-dawn water potential value recorded for the non-irrigated plot was -0.94 MPa in October 1991. The lowest mean water

potential value recorded for the irrigated plot was -1.62 MPa in October 1991 in the upper portion of the crown. The lowest mean water potential value recorded for the non-irrigated plot was -1.75 MPa in October 1991 in the upper portion of the crown.

A trend of more negative water potential with increasing height in crown position was observed. This trend is explained by the hydrostatic gradient that exists in the tree which helps in the movement of water from the roots to the leaves in the upper part of the canopy. This trend has been observed in other species of conifers and loblolly pine (Scholander et al. 1965, Rogers et al. 1975, Hellkvist 1974, Chapman 1990).

Air Temperature and Vapor Pressure Deficit

Air temperature increased diurnally from a lower pre-dawn value to a higher value in the middle of the day. Vapor pressure deficit followed the pattern of air temperature. The vapor pressure deficit increased diurnally from a lower pre-dawn value to a higher value in the middle of the day (fig. 7-14). Vapor pressure deficit increases with increase in temperature. It has been observed that air temperature and vapor pressure are highly correlated (Leverenz 1980).

Temperature and vapor pressure deficit vary depending on the time and season of measurement. Temperature did not

vary between the 1990 and 1991 flush. Temperature was highest in the upper portion of the crown and it decreased with decreasing crown position. This trend was observed by other researchers (Bergen 1974, Chapman 1990). The temperature recorded in the month of July was the highest and it kept decreasing as fall progressed. This decrease in temperature was due to the lower angle of the sun and the reduction in the amount of radiant energy falling on the needles.

Vapor pressure deficit did not differ between the 1990 and 1991 flush. Vapor pressure deficit was highest in the upper portion of the crown and it decreased with decreasing crown position. Vapor pressure deficit differed depending on the season of measurement. Vapor pressure deficit was highest in the month of October compared to all the other months. Niether temperature nor vapor pressure deficit varied between irrigated and non-irrigated treatments. It has been observed in other studies that vapor pressure deficit increased at the end of the growing season and vapor pressure deficit also increased with increase in temperature (Hodges 1966, Fites and Teskey 1988, Teskey et al. 1984, Teskey et al. 1987).

Chlorophyll Content

The figures 15-16 depict the total chlorophyll and chlorophyll a content for each age-flush class and crown position for each measurement day in the irrigated and non-

irrigated plots. There was seasonal variation in the pigment content. During the month of August the chlorophyll content was high in both the irrigated and the non-irrigated plots. The chlorophyll content was high in summer and declined as winter approached. This trend of a high chlorophyll content in summer and a decline in winter has been noticed in other conifers and loblolly pine seedlings (Bourdeau 1959, McGregor and Kramer 1963, Lewandowska and Jarvis 1977). According to Higginbotham (1974), there was no decline in chlorophyll content in winter. The decline in chlorophyll content is due to the frost and this decline first occurred on the needles exposed to sunlight and the needles that were in shade were affected later (Perry and Baldwin 1966). The increased chlorophyll content in summer helps in the better absorption of light and hence a better photosynthetic rate and increased tree productivity.

In this study the chlorophyll content did not vary between crown positions. Similar results have been observed in other species of conifers (Lewandowska and Jarvis 1977, Lewandowska et al. 1977). The results obtained here are different from the results obtained by some other researchers working with loblolly pine trees and seedlings and also with other coniferous seedlings (Bourdeau and Laverick 1958, Higginbotham 1974, Cregg 1990). These researchers reported that shading increases the amount of chlorophyll content present in the needles.

The values obtained for chlorophyll content were similar to the values obtained by Chapman (1990).

A general trend observed here was that the younger flush had a lower chlorophyll content compared to the older flush. Similar results have been observed by other researchers in loblolly pine and other species of conifers (Higginbotham 1974, Vapaavuori and Vuorinen 1989).

Photosynthetic Photon Flux Density and Carbon Exchange Rate

The figures 17-24 depict the photosynthetic photon flux densities for each age-flush class and crown position in both the irrigated and non-irrigated plots. On clear days photosynthetic photon flux density varied diurnally from a lower pre-dawn value to a higher value by late afternoon. The pattern of photosynthetic photon flux density depends on the season of measurement. The photosynthetic photon flux density was highest in the upper portion of the crown and the photosynthetic photon flux density decreased with the depth of the canopy. The photosynthetic photon flux density was highest on the youngest foliage because they were present on the outermost edge of the crown. The photosynthetic photon flux density in the middle portion and lower portion of the canopy were less than in the upper portion of the canopy. Brooks et al. (1991), reported that photosynthetic photon flux density decreased from 1500 μmol $m^{-2}s^{-1}$ at the top of the

canopy to 3 μmol $m^{-2}s^{-1}$ at the ground level. The sharp gradient led to changes in shoot and foliar morphology. It has also been reported that with increase in the depth of the canopy the light intensity decreases (Kramer and Kozlowski 1979, Lewandowska and Jarvis 1977, Lewandowska et al. 1977, Troeng and Linder 1982b).

In the irrigated plot the photosynthetic photon flux density received by the middle and lower portions of the crown over the growing season was 61% and 52%, respectively of the photosynthetic photon flux density received by the upper crown position (fig. 25). In April 1992, the photosynthetic photon flux density received by the middle and lower portions of the crown for the irrigated trees was 76% and 63%, respectively of the photosynthetic photon flux density received by the upper crown position.

In the non-irrigated plot the photosynthetic photon flux density received by the middle and lower portions of the crown over the growing season was 45% and 58%, respectively of the photosynthetic photon flux density received by the upper crown position (fig. 25). In April 1992, the photosynthetic photon flux density received by the middle and lower portions of the crown was 69% and 63%, respectively, of the photosynthetic photon flux density received by the upper crown position.

The values obtained for the whole season in the irrigated plot were similar to the values obtained by Chapman (1990), who reported that the photosynthetic photon

flux density of the middle and lower portions of the crown was 57% and 39%, respectively of the photosynthetic photon flux density received by the upper crown position. There was a discrepancy in the photosynthetic photon flux density values obtained for the whole season in the non-irrigated plot. The values obtained showed that the photosynthetic photon flux density values obtained in the lower portion of the crown was higher than the photosynthetic photon flux density values obtained in the middle portion of the crown. This may be due to the very high values of photosynthetic photon flux density obtained during some of the measurements during the later part of the day in July for the lower portion of the crown (fig. 18).

The average light intensity obtained was highest in the month of July. The average light intensity over all age-flush classes obtained for the irrigated plot for the upper crown position was 380.95 μmol $m^{-2}s^{-1}$, and it was 301.77 and 156.03 μmol $m^{-2}s^{-1}$ for the middle and lower crown positions, respectively. The average light intensity over all age-flush classes obtained for the non-irrigated plot for the upper crown position was 586.44 μmol $m^{-2}s^{-1}$, and it was 196.68 and 475.29 μmol $m^{-2}s^{-1}$ for the middle and lower crown positions, respectively. In August the measurements were made on a cloudy day and the values obtained were very low and hence the percent photosynthetic photon flux density obtained for the middle and lower crown positions were not very different from the upper crown

position. The average light intensity decreased during the month of October. The average light intensity over all age-flush classes obtained for the irrigated plot in the month of October in the upper crown position was 341.85 μmol $m^{-2}s^{-1}$, and it was 127.39 μmol $m^{-2}s^{-1}$ and 115.82 μmol $m^{-2}s^{-1}$ for the middle and lower crown positions. The average light intensity over all age flush classes obtained for the non-irrigated plot for the upper crown position was 337.80 μmol $m^{-2}s^{-1}$, and it was 207.19 and 77.96 μmol $m^{-2}s^{-1}$ for the middle and lower crown positions respectively. In October there was a decrease in the values obtained for light intensity because of the decrease in the angle of the sun and the mutual shading by the adjacent trees. April 1992 was the beginning of the growing season and the light intensity was high and hence the increase in the percent of photosynthetic photon flux density in the middle and lower positions of the crown. The increase in light intensity in the middle and lower positions of the crown was due to the increased angle of the sun and the increased amount of radiant energy falling on the needles. Also, the needles that were measured were the 1991 needles which were present on the outer edge of the canopy and hence had a reduced amount of shading.

The figures 17-24 also depicts the carbon exchange rate for each age-flush class and crown position in both the irrigated and non-irrigated plots. The daily carbon exchange rate increased diurnally from a low value in the

morning to a high value by mid-afternoon. This pattern of carbon exchange rate is similar to the patterns observed by other researchers in loblolly pine and other species of conifers (Helms 1965, Hodges 1966, Schulze 1977, Leverenz 1980, Troeng and Linder 1982, Beadle et al. 1985, Jarvis and Sanford 1986, Boltz et al. 1986, Fites and Teskey 1988, Chapman 1990, Cregg 1990). The carbon exchange rate values are similar to the values obtained by some of the researchers using loblolly pine trees and seedlings (Boltz et al. 1986, Fites and Teskey 1988, Cregg 1990, Chapman 1990).

In this study the carbon exchange rate measurements in general were obtained four times a day starting with a pre-dawn respiration measurement, and then at intervals of three hours starting from 8.00 a.m till 5.00 p.m. But in some of the experiments photosynthesis has been monitored all through the day and the pattern of net assimilation occurs with rapid fluctuations. In the middle of the day there appears to be a 'mid-day depression in photosynthesis'. This mid-day depression of photosynthesis has been associated with high temperature stress or water stress. These fluctuations may be an inherent function of the photosynthesis mechanism or a direct result of changes in the internal status of the trees (Helms 1965, Hodges 1967, Hari and Luukkanen 1973).

The highest photosynthetic rate obtained in this study was in the month of July. This was because of the high

light intensity during this month. McGregor and Kramer (1963) found for loblolly pine seedlings that peak photosynthesis per unit of fascicle length occurred in May. Higginbotham (1974) found that peak photosynthesis occurred in late spring and early summer. Linder and Troeng (1982) found that there was a variation in needle development and difference in the attainment of photosynthetic capacity. Hence, attainment of peak photosynthetic rate depended on a number of factors and it also varied depending on the environmental conditions for that growing season. Hence, in determining the peak photosynthetic rate the environmental factors should be taken into consideration.

High photosynthetic rates were obtained in the month of April 1992 because of the high light intensities obtained during this month and also it was the beginning of the growing season. During this month the trees were in the flowering stage. The process of flowering acted as a large sink for the photosynthates. The photosynthetic rates obtained during August was very low because of cloudiness during the measurement day.

The only month where there was a difference in photosynthetic rate between the irrigated and non-irrigated plots was in the month of October. In the other months the moisture stress was not enough to bring about any differences in photosynthetic rates between the irrigated and non-irrigated plots. In this study water stress did not affect the photosynthetic rate. Perhaps the water

stress was not sufficient to bring about a reduction in photosynthetic rate or the trees have developed a mechanism to counteract the stress and still maintain a high photosynthetic rate. The photosynthetic rate in the non-irrigated plot was almost equal to the photosynthetic rate in the irrigated plot. The other possible reason could be that the water potential did not decrease below the threshold or critical water potential level for the physiological processes to be affected.

The photosynthetic rate did not differ significantly between the 1990 and 1991 flush. The only trend that was observed was that the younger foliage photosynthesized at a higher rate compared to the older foliage. The trend observed here was very similar to the one noticed by Reynolds et al. (1980), where he reported that the needles formed in the previous year contributed to a maximum extent to the carbon gain that occurred between April and August. The current year's foliage developed a peak photosynthetic capacity slowly and later in the growing season. Teskey et al. 1984, noticed older needles contributed to maximum extent to carbon gain and current foliage developed slowly and later towards the growing season.

The photosynthetic rate of the upper, middle and lower crown position varied. In general, the upper crown position photosynthesized at a higher rate compared to the middle crown position, which photosynthesized at a higher rate compared to lower crown position. Linder and Troeng

(1982a), also found this difference when they were working with Scots pine (Pinus sylvestris L). The reason for this variation in photosynthetic rate between crown positions may be due to the variation in photosynthetic photon flux density penetration into the canopy, the angle of the sun and the distribution of the foliage. Other researchers have also reported this pattern in other species of conifers (Jarvis and Sanford 1977, Beadle et al. 1982a). The decrease in the photosynthetic rate in the lower portions of the crown may be due to the lower photosynthetic capacity of the needles and also the morphological and physiological adaptation to low light conditions (Lewandowska et al. 1977).

In the irrigated plots photosynthesis continued to occur at a higher rate even at the end of the day. In the non-irrigated plot photosynthesis did not occur at as high a rate at the end of the day. This might be due to the presence of increased amount of moisture in the soil in the irrigated plot which facilitates photosynthesis to occur at a higher rate (fig. 17-24).

It has been reported that photosynthetic rate decreased with a decrease in xylem pressure potential below a critical value in loblolly pine seedlings (Brix 1962, Seiler and Johnson 1988). A reduction in xylem pressure potential below a critical value leads to a decrease in the photosynthetic rate in a number of other species of conifers (Brix 1977, Beadle et al. 1981).

In the irrigated plot the photosynthetic rate of the middle and lower portions of the crown was 66% and 54% of the photosynthetic rate obtained by the upper crown portion. For the month of April 1992, the photosynthetic rate of the middle and lower portions of the crown was 80% and 56% of the photosynthetic rate obtained by the upper crown portion. In the non-irrigated plot the photosynthetic rate of the middle and lower portions of the crown was 61% and 50% of the photosynthetic rate obtained by the upper crown portion. For the month of April 1992, the photosynthetic rate of the middle and lower portions of the crown was 75% and 62% of the photosynthetic rate obtained by the upper crown portion (fig. 26). The values obtained for the whole season in the irrigated and non-irrigated plot are less than the values obtained by Chapman (1990), who reported that the photosynthetic rate of the middle and lower portions of the crown was 82% and 52%, respectively, of the photosynthetic rate obtained by the upper crown portion. The values obtained in this study are closer to the values obtained by Higginbotham (1974), who found that the photosynthetic rate of the middle and lower portions of the crown was 76% and 51%, respectively, of the photosynthetic rate obtained by the upper crown portion.

Dark respiration in general increased diurnally from a lower value in the morning to a higher value in the middle of the day and decreased again in the evening (fig. 27-30). The dark respiration rate did not differ between age-flush

classes, crown position and between irrigated and non-irrigated plots. Dark respiration did not vary throughout the study period. The results obtained in this study are contradictory to the results obtained in other studies involving dark respiration. Brix (1960), reported that in loblolly pine seedlings the respiration rate decreased initially with an increase in water stress and later on increased as the water stress increased. Respiration was limited by a chemical process rather than by limited oxygen supply. It has been reported that with increase in water stress the dark respiration decreased (Puritch 1973, Melzak et al. 1985). The rate of dark respiration varied depending on the season of growth (McGregor and Kramer 1963). It has been reported that respiration differs between age flush classes and also between crown positions. The younger foliage respired at a higher rate than the older foliage. The foliage in the upper crown position had a higher rate of dark respiration than the foliage in the middle or lower crown portions (Brooks et al. 1991). It has been reported that the rate of dark respiration is highly related to temperature (Brooks et al. 1991, Mebrahtu et al. 1991).

Respiration values obtained in this study were higher than the values obtained in other studies using loblolly pine. In this study the values ranged between 0.10 to 2.50 μmol $m^{-2}s^{-1}$. Cregg et al. (1990), obtained respiration rates of 0.10 to 0.40 μmol $m^{-2}s^{-1}$ when they were developing

light response curves in loblolly pine trees. Drew and Ledig (1981), obtained respiration rates of 1.50 to 5.50 mg Co_2 $h^{-1}g^{-1}$ shoot dry weight in loblolly pine. Melzack et al. (1985), obtained respiration values of 0.40 to 1.00 μmol $m^{-2}s^{-1}$ when they were working on Pinus halapensis in Israel. Puritch (1973), obtained respiration values of 0.24 to 4.77 μmol $m^{-2}s^{-1}$ in four species of Abies. Brooks et al. (1991), obtained values of 0.38 to 4.30 μmol $m^{-2}s^{-1}$ in Pacific silver fir. Mebrahtu obtained values of 0.50 to 4.00 μmol $m^{-2}s^{-1}$ in Black locust.

Xylem Pressure Potential and Stomatal Conductance

The figures 31-38 depict the xylem pressure potential for each age-flush class and crown position in both the irrigated and non-irrigated plots. The xylem pressure potential decreased diurnally from a higher pre-dawn value to a lower value in the middle of the day. The daily pattern of xylem pressure is similar to that observed in the other species of conifers (Hellkvist 1974, Leverenz 1981, Beadle et al. 1985a, Teskey et al. 1984).

The figures 31-38 also depict the stomatal conductance for each age-flush class and crown position in both the irrigated and non-irrigated plots. The stomatal conductance increased diurnally from a lower pre-dawn value to a higher value in the middle of the day and decreased again in the late afternoon. In general, stomatal

conductance did not differ between age-flush classes, crown positions or between irrigated and non-irrigated plots. The only month in which there was a difference in stomatal conductance between treatments was in the month of October. High values of stomatal conductance were obtained during the pre-dawn measurements in July. This pattern of high pre-dawn stomatal conductance values has been observed by Beadle et al. (1985b) when they were working on Scots pine.

The diurnal pattern of stomatal conductance obtained in this study was similar to that observed by other researchers (Bates and Hall 1981, Dougherty and Hinckley 1981, Gollan et al. 1985, Leverenz 1981, Turner et al. 1985b, Beadle et al. 1985a, Fites and Teskey 1988).

The results obtained concerning stomatal conductance and water potential are contradictory to the results obtained in other studies. Beadle et al. (1985a), reported that the stomatal conductance was higher in the top level than at the middle level and higher at the middle level than at the lower level. Similar results have been reported by other researchers (Troeng and Linder 1982b, Kull and Koppel 1987, Cregg 1990). In some of the other studies it has been shown that the relationship between water potential and stomatal conductance is not well defined and stomatal conductance is independent of water potential (Leverenz 1980, Beadle et al. 1985b). In other studies it was concluded that leaf conductance, transpiration rate and net photosynthetic rate did not have

any relationship with leaf water potential but they were all highly correlated to soil water status (Bates and Hall 1981, Gollan et al. 1985, Turner et al. 1985b). As xylem pressure potential decreases stomatal conductance decreases (Teskey et al. 1986). In a water stress study with red spruce seedlings it was concluded that decrease in photosynthesis due to water stress was highly related to decrease in stomatal conductance and that photosynthesis was restricted due to the lack of carbon-dioxide (Seiler and Cazell 1990). Stomatal conductance values obtained were similar to the values obtained by other researchers working on loblolly pines (Cregg 1990, Teskey et al. 1987, Teskey et al. 1986). The values obtained ranged between 0.01 to 0.60 mol $m^{-2}s^{-1}$. The higher values were obtained during the pre-dawn determination of stomatal conductance.

Vapor Pressure Deficit and Stomatal Conductance

The figures 39-46 depict vapor pressure deficit and stomatal conductance for each age-flush class and crown position in both the irrigated and non-irrigated plot. The vapor pressure deficit increased diurnally from a lower pre-dawn value to a higher value in the middle of the day. This pattern is similar to the results obtained in other studies (Fites and Teskey 1988, Teskey et al. 1987). Vapor pressure deficit did not differ statistically between age-flush classes and between crown positions and between the

irrigated and non-irrigated plots. The only trend noticeable is that the vapor pressure deficit was highest in the upper portion of the crown position and decreased with decreasing crown position.

The results obtained indicate that stomatal conductance is affected to large extent by vapor pressure deficit. With an increase in vapor pressure deficit there was a decrease in stomatal conductance. This is due to the closure of stomata at very high vapor pressure deficit. It has been shown in other studies that an increase in vapor pressure deficit leads to a decrease in stomatal conductance (Gollan et al. 1985, Grien et al. 1988). It has also been reported that photosynthetic photon flux density and vapor pressure deficit are primary factors controlling stomatal function and temperature and water deficits are secondary factors controlling stomatal conductance (Kaufmann 1982).

It has been reported in other studies that stomatal conductance is affected to a large extent by vapor pressure deficit (Leverenz 1980, Leverenz 1981, Beadle et al. 1985b). Stomatal conductance was affected at lower vapor pressure deficits but at larger vapor pressure deficits was not affected. The result obtained here is similar to the results reported by Beadle et al. 1985b in Scots pine.

Diurnal variation during the month of August was not high. This was because the measurement day was cloudy and

vapor pressure was strongly limiting. This is similar to the pattern obtained by Leverenz (1981) in Douglas fir.

Photosynthetic Photon Flux Density and Stomatal Conductance

The figures 47-54 depict the photosynthetic photon flux density and stomatal conductance for each age-flush class and crown position in both the irrigated and non-irrigated plots. The photosynthetic photon flux density varies diurnally from a lower pre-dawn value to a higher value by late afternoon. The pattern of photosynthetic photon flux density depends on the season of measurement. The photosynthetic photon flux density was highest in the upper portion of the crown and decreased with the depth of the canopy. The photosynthetic photon flux density was highest on the youngest foliage because of their presence on the outer edge of the crown. The light intensity in the middle and lower portion of the canopy are lower compared to the upper portion of the crown. This is similar to the trend observed by other researchers (Kramer and Kozlowski 1979, Lewandowska and Jarvis 1977, Lewandowska et al. 1977, Troeng and Linder 1982b, Brooks et al. 1991).

The results for stomatal conductance indicate that photosynthetic photon flux density does not have a very good relationship with stomatal conductance. The results obtained here for stomatal conductance are contradictory to the results observed in other studies. Kaufmann (1982),

proposed that photosynthetic photon flux density and vapor pressure deficit are the important primary factors controlling stomatal function. In this study there was no variation in stomatal conductance between age-flush classes and there was no variation in stomatal conductance between crown positions or between the irrigated and non-irrigated plots. Leverenz and Jarvis (1979), proposed that sun needles had a higher rate of stomatal conductance than shade needles in Sitka spruce. In another study on Scots pine, stomatal conductance declined with depth in the canopy and also the diurnal course of stomatal conductance was not very well related to light intensity (Beadle et al. 1985a).

Regression Models

Regression models were developed using the stepwise backward linear regression procedure. Regression models were developed for each month and also for the whole set of measurements.

Photosynthesis

July 11, 1991

The regression model for July contained the variables light, DV2position, and humidity (Table. 1). The r-square value for this model was 0.58. Light was positively and highly related to photosynthesis. The model showed that

with increase in light there was an increase in photosynthesis when all the other factors were kept constant (fig. 17-18). The middle portion of the crown had a higher photosynthetic rate compared to the lower crown position. This was because of the increased amount of irradiance falling on the needles present in the middle crown position and also due to the reduced amount of shading from the adjacent trees (fig. 25). Humidity was inversely related to photosynthesis, i.e, with increase in humidity photosynthesis decreased when all other factors were kept constant. During the month of July light and crown position were the important variables highly related to photosynthesis. Humidity was another variable related to photosynthesis. These three variables accounted for about 58% of the variation in photosynthesis. These results are similar to the results obtained by other researchers working on loblolly pine and other species of conifers (Lewandowska et al. 1977, Leverenz 1980, Leverenz and Jarvis 1980, Linder and Troeng 1982b, Beadle et al. 1985a, 1985b, Jarvis and Sanford 1986, Teskey et al. 1986, 1987, Kull and Koppel 1987, Cregg et al. 1990).

August 21, 1991

The regression model for August contained the variables light, total chlorophyll and DVirrigation (Table. 1). The r-square value for this model was 0.52. Light was positively and highly related to photosynthesis. The model

showed that with increase in light there was an increase in photosynthesis when all other factors are kept constant. Light was very low on the day of measurement. Total chlorophyll was negatively related to photosynthesis i.e, with increase in chlorophyll content photosynthesis decreases. The total chlorophyll content was slightly higher in August compared to the other months (fig. 15-16). This inverse relationship does not usually occur. Irrigation was also negatively related to photosynthesis. These relationships may be due to cloudiness on the day of measurement (fig. 19-20), and due to the very slight variation in temperature and vapor pressure deficit (fig. 9-10).

October 10, 1991

The regression model for October contained the variables light, water potential, DV2position, DVirrigation, and vapor pressure deficit (Table. 1). The r-square value for this model was 0.53. Light was positively related to photosynthesis. The model showed that with an increase in light there was an increase in photosynthesis when all other factors were held constant (fig. 11-12). This is similar to the results obtained by Beadle et al. (1985a), (1985b), and Cregg et al. (1990). Water potential was negatively related to photosynthesis. This means that at more negative water potentials there was an increase in photosynthetic rate. This was because as

the day progressed the xylem pressure decreased but photosynthesis was being carried out at a higher rate (fig. 5, fig. 21, 22). The middle crown position had a higher photosynthetic rate compared to the lower crown position. This was because of the increased amount of irradiance falling on the needles present in the middle crown position (fig. 25). This was because of the senescence of the older needles in the canopy. The irrigated plot had a higher photosynthetic rate compared to the non-irrigated plot. This is the only month in the study period wherein there was a plot difference. The irrigated plot photosynthesized at a higher rate compared to the non-irrigated plot because of the presence of increased amount of moisture in the soil and it was also observed that the trees in the irrigated plot continued to photosynthesize at a higher rate even at the end of the day compared to the non-irrigated plot (fig. 21, 22). Vapor pressure deficit was negatively related to photosynthesis. This means that with increase in vapor pressure deficit the photosynthetic rate decreased when all other factors are kept constant. Generally photosynthesis increases with increase in vapor pressure deficit but beyond a certain amount of vapor pressure deficit photosynthesis starts to decrease. The above explained variables accounted for about 53% of the variation in photosynthesis.

April 8, 1992

The regression model for the month of April contained the variables light, DV2position, vapor pressure deficit, and humidity (Table. 1). The r-square value for this model was 0.81. In this month the measurements were obtained on needles of the 1991 flush. Light was positively related to photosynthesis. The model shows that with increase in light there is an increase in photosynthesis when all other factors are kept constant. These results are similar to the results obtained by Beadle et al. (1985a), (1985b), Teskey et al. (1986), Cregg et al. (1990). The middle crown position had a higher photosynthetic rate compared to the lower crown position. This was because of the increased amount of irradiance falling on the needles present in the middle crown position and also due to the reduced amount of shading by the developing needles. Vapor pressure deficit and humidity are negatively related to photosynthesis. Increase in vapor pressure deficit leads to a decrease in photosynthesis when all other factors are held constant. Increase in humidity leads to a decrease in photosynthesis when all other factors are held constant These four variables account for about 80% of the variation in photosynthesis.

Seasonal Model

The regression model for the whole study period contained the variables light, water potential, air

temperature, DV2position, vapor pressure deficit, humidity, DVJul, and DVAugust (Table. 1). The r-square value for this model was 0.59. Increase in light leads to an increase in photosynthesis. Higher photosynthetic rates were noticed at more negative water potentials, hence a negative relationship. Increase in air temperature leads to a decrease in photosynthesis. This was due to the increased vapor pressure deficit caused by the increase in air temperature and this leads to a partial closure of the stomata which leads to a reduction in the photosynthetic rate. The middle crown position has been an important position in the canopy because it has been photosynthesizing at a higher rate compared to the lower crown position. The middle crown position photosynthesized at a higher rate because of the slight shading of the needles which reduced the amount of heat falling on the needles and hence a reduced loss of water. Vapor pressure deficit was negatively related to photosynthesis. With an increase in vapor pressure deficit there is a decrease in photosynthesis when all other factors are held constant. An increase in vapor pressure leads to a slight closure of the stomata which leads to a decrease in photosynthesis. Humidity was negatively related to photosynthesis. With an increase in humidity there is a decrease in photosynthesis. In July and August the photosynthetic rates were different compared to the month of October. All the variables explained about 59% of the variation in photosynthesis.

Stomatal Conductance

July 11, 1991

The regression model for July contained variables as light, water potential, air temperature, vapor pressure deficit, and humidity (Table. 2). The r-square value for this model was 0.69. Light was negatively related to conductance. Light was not strongly related to conductance. In this study stomatal conductance showed only a slight relationship with change in light (fig. 47-48). This was similar to the results obtained by Beadle et al. (1985a) in Scots pine. Water potential had a negative relationship with conductance. Stomatal conductance was high at more negative water potentials. Even the photosynthetic rates were higher at more negative water potentials. Hence there was a negative relationship between water potential and stomatal conductance. Vapor pressure deficit had a positive relationship with conductance. Increase in vapor pressure deficit leads to an increase in stomatal conductance when all the other factors were kept constant. In this study stomatal conductance was highly related to vapor pressure deficit. Beadle et al. (1985b), reported that the major determinant of stomatal conductance was vapor pressure deficit.

Humidity had a positive relationship with conductance. Increase in humidity leads to an increase in conductance when all other factors were kept constant. Water

potential, air temperature, vapor pressure deficit, and humidity exhibit a very strong relationship with conductance. The above explained variables account for about 69% of the variation in stomatal conductance.

August 21, 1991

The regression model for August contained the variables light, total chlorophyll, air temperature, vapor pressure deficit, and humidity (Table. 2). The r-square value for this model was 0.47. Light was positively related to conductance, i.e, with increase in light there will be an increase in conductance when all other factors are kept constant. Light was not strongly related to stomatal conductance. Total chlorophyll was positively and strongly related to conductance. Air temperature was positively and strongly related to conductance. Vapor pressure was negatively and highly related to conductance. Humidity was negatively related to conductance. This unusual relationship between vapor pressure deficit and stomatal conductance and between humidity and stomatal conductance may be because of cloudiness on the day of measurement. The above mentioned variables account for about 46% of the variation in stomatal conductance.

October 10, 1991

The regression model for October contained the variables water potential, DV1position, DVirrigation, vapor

pressure deficit, and humidity (Table. 2). The r-square value for this model was 0.65. Water potential was negatively related to conductance. Higher stomatal conductance values were obtained at lower water potentials (fig. 43-44). The upper portion of the crown had a different conductance compared to the lower crown position. The irrigated plot had a higher conductance compared to the non-irrigated plot. At less negative water potentials stomatal conductance values are higher. Hence a higher stomatal conductance was seen in the irrigated plot compared to the non-irrigated plot. Teskey et al. (1987), reported that in loblolly pine seedlings at less negative water potential stomatal conductance was higher. Vapor pressure deficit was positively related to conductance. In this study vapor pressure deficit was highly related to stomatal conductance. Beadle et al. (1985b), reported that the stomatal conductance was determined to large extent by vapor pressure deficit.

Humidity was positively related to conductance. Vapor pressure deficit and humidity were highly related to stomatal conductance. The above explained variables accounted for about 65% of the variation in stomatal conductance.

April 8, 1991

The regression model for the month of April contained the variables air temperature, vapor pressure deficit, and

humidity (Table. 2). The r-square value for the model was 0.38. Air temperature was negatively and strongly related to stomatal conductance. With an increase in air temperature stomatal conductance decreased when all the other factors were kept constant. An increase in air temperature leads to an increase in vapor pressure deficit (fig. 11-12), and this leads to a slight decrease in stomatal conductance. Vapor pressure deficit was positively related to conductance. An increase in vapor pressure deficit leads to an increase in stomatal conductance. Humidity was positively related to conductance. Vapor pressure deficit and humidity were highly related to stomatal conductance. The above explained variables accounted for about 38% of the variation in stomatal conductance.

Seasonal model

The regression model for the whole study period contained variables water potential, vapor pressure deficit, humidity, DVJuly, and DVAug (fig. 2). The r-square value for the whole model was 0.48. Water potential was strongly and negatively related to conductance. This is because of the high stomatal conductance values at higher negative water potential values. Vapor pressure deficit was positively related to conductance. Stomatal conductance was strongly determined by vapor pressure deficit. Humidity was positively related to conductance.

An increase in humidity leads to an increase in stomatal conductance when all the factors are kept constant. This can occur only to a particular level but at very high humidity levels stomatal conductance decreases. The conductance for the month of July and August was different from the conductance rate for the month of October. The above explained variables account for about 48% of the variation in stomatal conductance.

CHAPTER IV

CONCLUSION

The objective of this study was to quantify the effects of moisture stress on photosynthesis, respiration and stomatal conductance. The hypotheses for this study were that low soil moisture, high evaporative demand, shading, and high temperature over extended periods decrease annual net carbon gain. The objective of this study was determined by taking measurements of photosynthesis, respiration and stomatal conductance during the dry periods of the growing season when there was a difference in moisture content between plots. The most important point that was noticed in this study was that even though there was a difference in moisture content between plots it was not sufficient to create a condition of marked stress to alter the processes of photosynthesis, respiration, and stomatal conductance. The only month in which there was a difference in photosynthetic rates between plots was in the month of October, when an apparent soil moisture difference between treatment plots was greatest.

Based on the analysis most of the variation in photosynthesis and stomatal conductance could be explained

by their strong relationships to variables such as quantum mean, water potential, air temperature, crown position, vapor pressure deficit, and humidity. Needles at the upper and middle crown positions were found to photosynthesize more than those at the lower crown position. The carbon exchange rates in the upper and middle crown positions are very important for the productivity of trees.

The carbon exchange rate and stomatal conductance did not vary between the upper and middle crown positions of the crown but were slightly higher than the lower crown position. The carbon exchange rate did not differ significantly between age-flush classes. The only trend was that the 1991 flush was photosynthesizing at a slightly higher rate compared to the 1990 flush. The carbon exchange rate did not differ between the irrigated and non-irrigated plots. The reason for this might be that the degree of stress established was not sufficient enough to create any change in the physiological processes. Perhaps the trees have developed a mechanism to counter act the stress and still maintain a high assimilation rate.

In the irrigated plot the photosynthetic photon flux density received by the middle and lower crown portions of the crown was 61% and 52%, respectively of the photosynthetic photon flux density received by the upper crown position. In the non-irrigated plot the photosynthetic photon flux density received by the middle and lower crown portions of the crown was 45 and 58%,

respectively of the photosynthetic photon flux density received by the upper crown position. In the irrigated plot the photosynthetic rate of the middle and lower portions of the crown was 66% and 54% of the photosynthetic rate obtained by the upper crown portion. In the non-irrigated plot the photosynthetic rate of the middle and lower portions of the crown was 61% and 50% of the photosynthetic rate obtained by the upper crown portion.

In general it can be concluded that lower soil moisture, high evaporative demand, shading, and high temperature over extended periods do reduce the annual net carbon gain of trees. These variables have a very strong relationship with photosynthesis and stomatal conductance.

The values of photosynthesis, respiration, and stomatal conductance obtained can be used to parameterize various models being developed by other researchers. Further study of these physiological processes is needed. The effect of moisture stress on these physiological processes could be better quantified if the study can be done in a drier year. Further study of the effects of moisture stress on physiological processes will help in the development of better forest management practices, and may provide insight into the potential response of forests to a changing climate.

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APPENDIXES

APPENDIX A

TABLES

TABLE I

REGRESSION MODELS FOR PHOTOSYNTHESIS

Month	Variable	Parameter	F-Statistics	Prob>F
July	Intercept	0.25466354	0.35	0.5545
	Quanmean	0.00390356	145.08	0.0001
	DV2position	0.75688405	10.97	0.0012
	Humidity	-0.01208548	3.56	0.0611
	R-square value:	0.57808662		
August	Intercept	-0.03438498	0.02	0.8942
	Quanmean	0.01241857	165.89	0.0001
	Totalchl	-0.96557787	3.03	0.0835
	DVirrigation	-0.35361701	6.96	0.0091
	R-square value:	0.51500883		
October	Intercept	-0.97480705	6.31	0.0129
	Quanmean	0.00446016	151.65	0.0001
	XPP	-0.10683022	7.51	0.0068
	DV2position	0.51000977	9.63	0.0022
	DVirrigation	0.43581949	5.29	0.0226
	VPD	-0.05732698	21.10	0.0001
	R-square value:	0.53100077		
April	Intercept	7.38387359	5.37	0.0239
	Quanmean	0.00646784	197.39	0.0001
	DV2position	0.91855759	6.70	0.0120
	VPD	-0.22704419	7.63	0.0076
	Humidity	-0.08403028	4.89	0.0308
	R-square value:	0.80586981		
Seasonal	Intercept	5.05471523	18.99	0.0001
	Quanmean	0.00506173	615.47	0.0001
	XPP	-0.05248633	5.92	0.0153
	Airtemp	-0.07973968	6.51	0.0110
	DV2position	0.53620338	26.53	0.0001
	VPD	-0.07480303	10.36	0.0014
	Humidity	-0.51914820	19.66	0.0001
	DVJul	1.02729231	13.41	0.0003
	DVAug	0.79007539	9.02	0.0028
	R-square value:	0.58899594		

TABLE II

REGRESSION MODELS FOR CONDUCTANCE

Month	Variable	Parameter	F-Statistic	Prob>F
July	Intercept	-1.06411545	9.17	0.0029
	Quanmean	-0.00005829	4.00	0.0475
	XPP	-0.01998239	16.46	0.0001
	Airtemp	-0.03505219	18.09	0.0001
	VPD	0.03290179	35.79	0.0001
	Humidity	0.02276568	56.74	0.0001
	R-square value:	0.69418144		
August	Intercept	-0.01045997	0.00	0.9802
	Quanmean	0.00008126	2.85	0.0930
	Totalchl	0.03539016	2.90	0.0905
	Airtemp	0.06548120	111.30	0.0001
	VPD	-0.06601458	24.27	0.0001
	Humidity	-0.01439139	8.09	0.0050
	R-square value:	0.46692824		
October	Intercept	-1.09775848	73.70	0.0001
	XPP	-0.00942588	6.72	0.0104
	DV1position	-0.03572947	7.77	0.0059
	DVirrigation	0.02893594	2.79	0.0966
	VPD	0.01434996	46.19	0.0001
	Humidity	0.01480177	124.31	0.0001
	R-square value:	0.65746255		
April	Intercept	-0.53866554	4.71	0.0337
	Airtemp	-0.03472564	22.64	0.0001
	VPD	0.04697770	24.78	0.0001
	Humidity	0.01415500	19.99	0.0001
	R-square value:	0.38754840		
Seasonal	Intercept	-0.60465302	54.71	0.0001
	XPP	-0.00354789	4.41	0.0363
	VPD	0.00662908	18.48	0.0001
	Humidity	0.00981782	108.65	0.0001
	DVJuly	-0.06771520	21.34	0.0001
	DVAugust	-0.16519412	203.52	0.0001
	R-square value:	0.48153790		

APPENDIX B

FIGURES

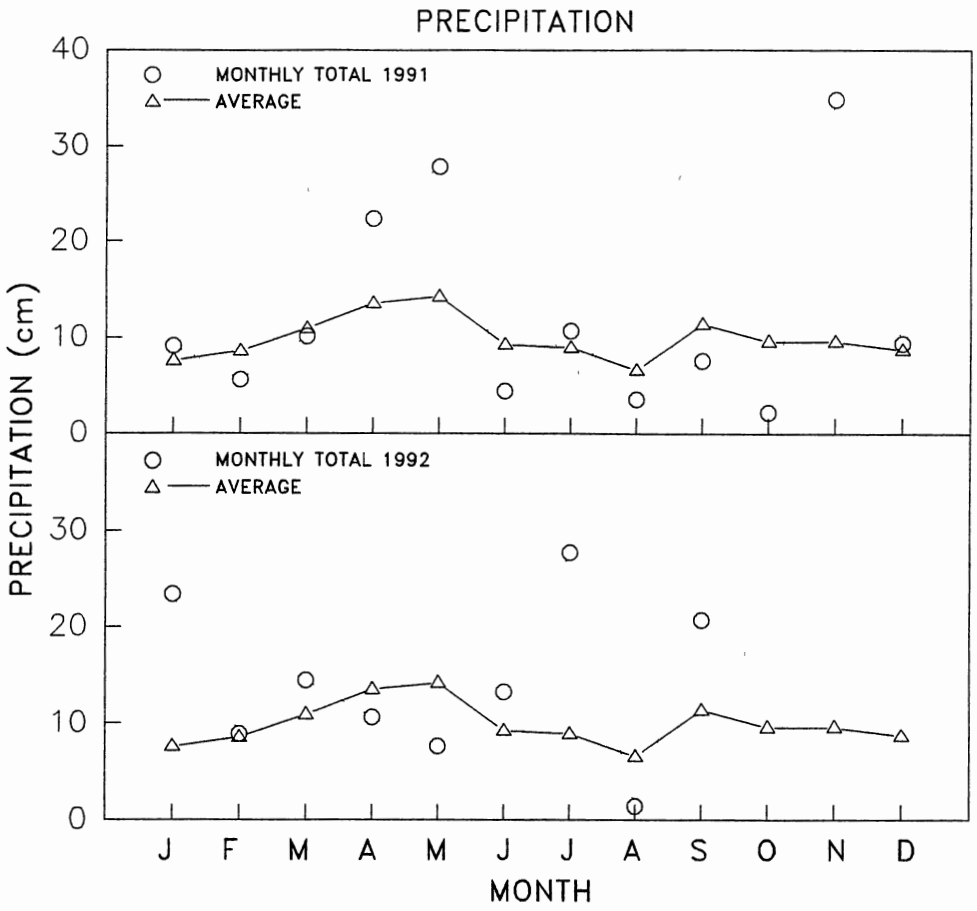

Figure 1. Monthly on-site precipitation for 1991 and 1992 and average monthly precipitation. Average monthly precipitation based on data recorded from 1951-1980 at Idabel.

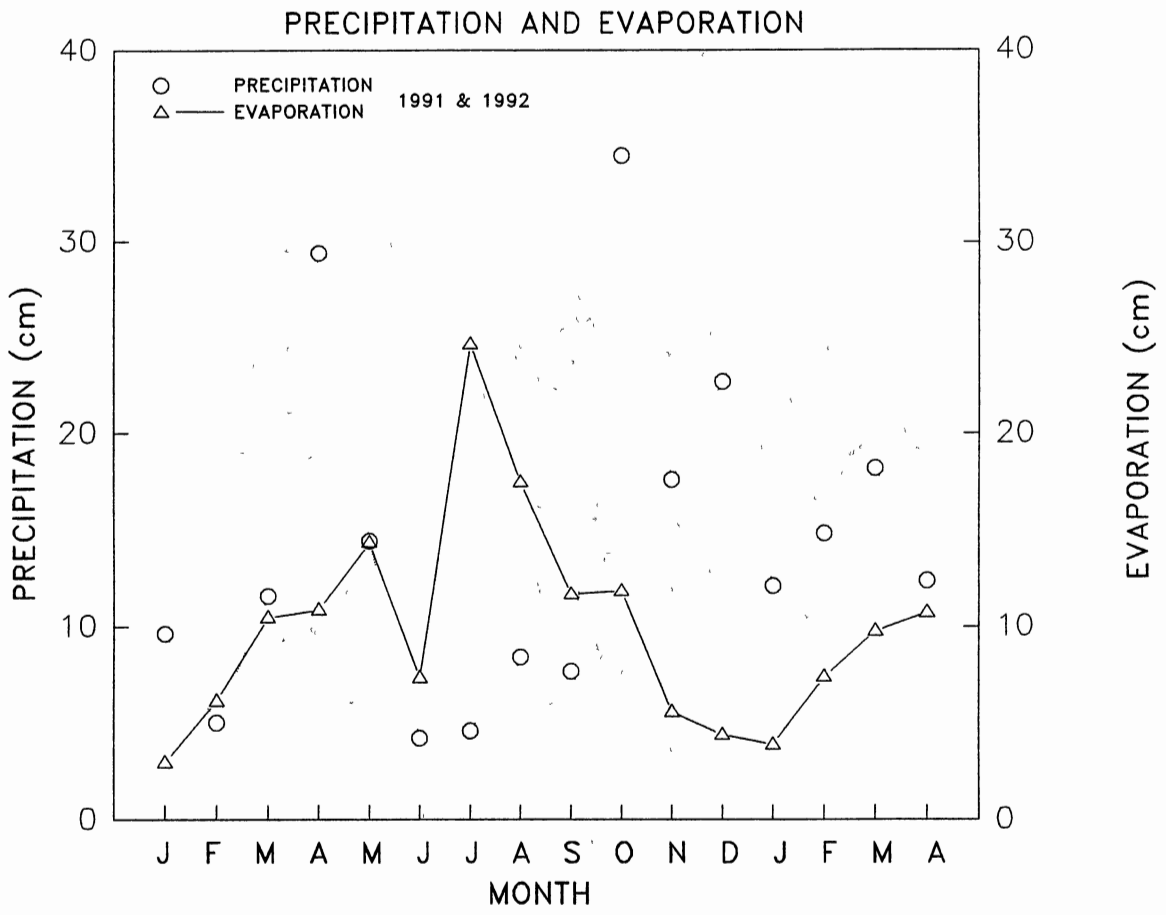

Figure 2. Monthly precipitation and pan evaporation for 1991 and 1992 from the Broken Bow Dam, 27 km north of the study site.

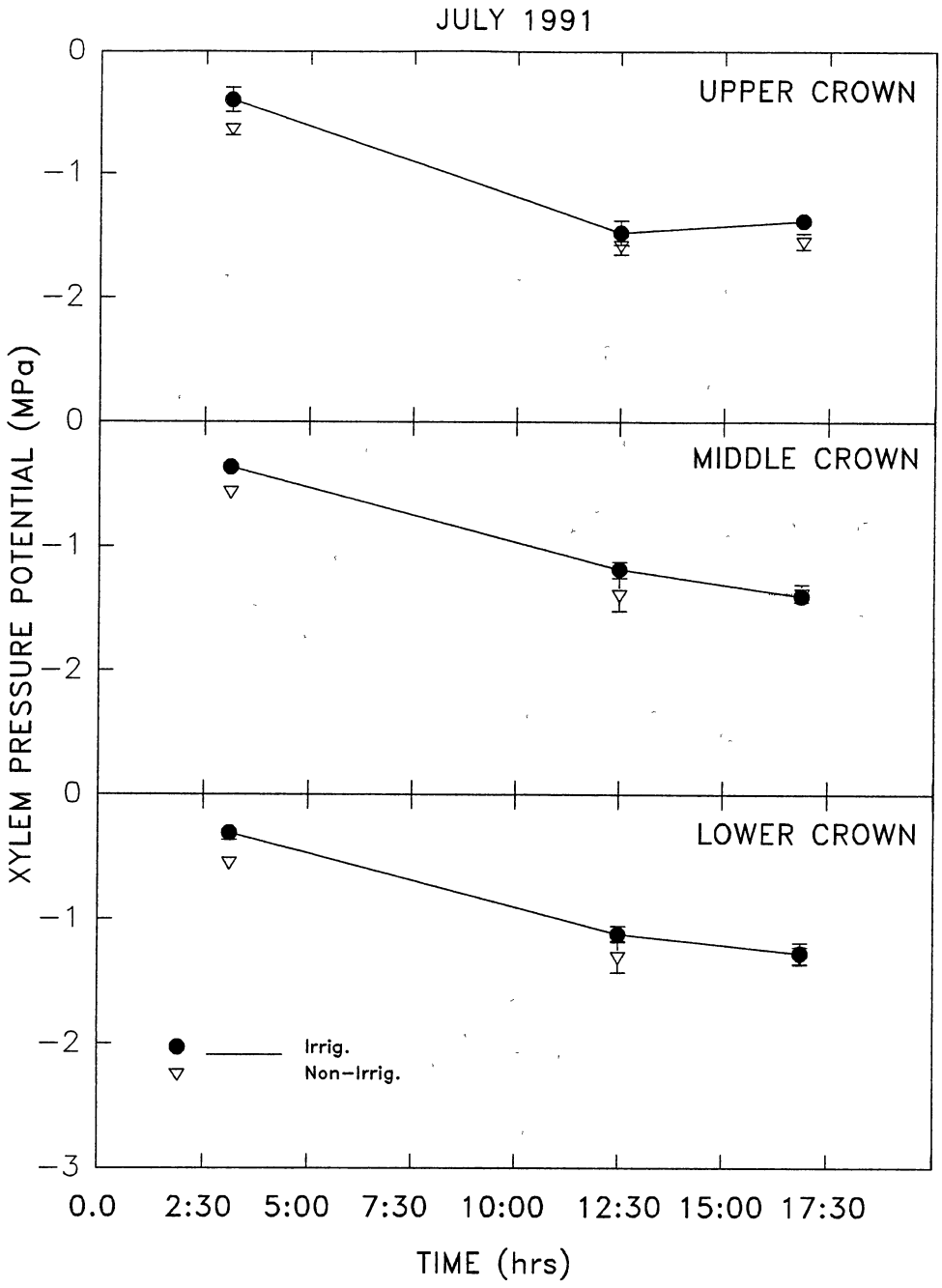

Figure 3. Diurnal patterns of xylem pressure potential for July. Each bar indicates one standard error and each point indicates the mean of three trees measured.

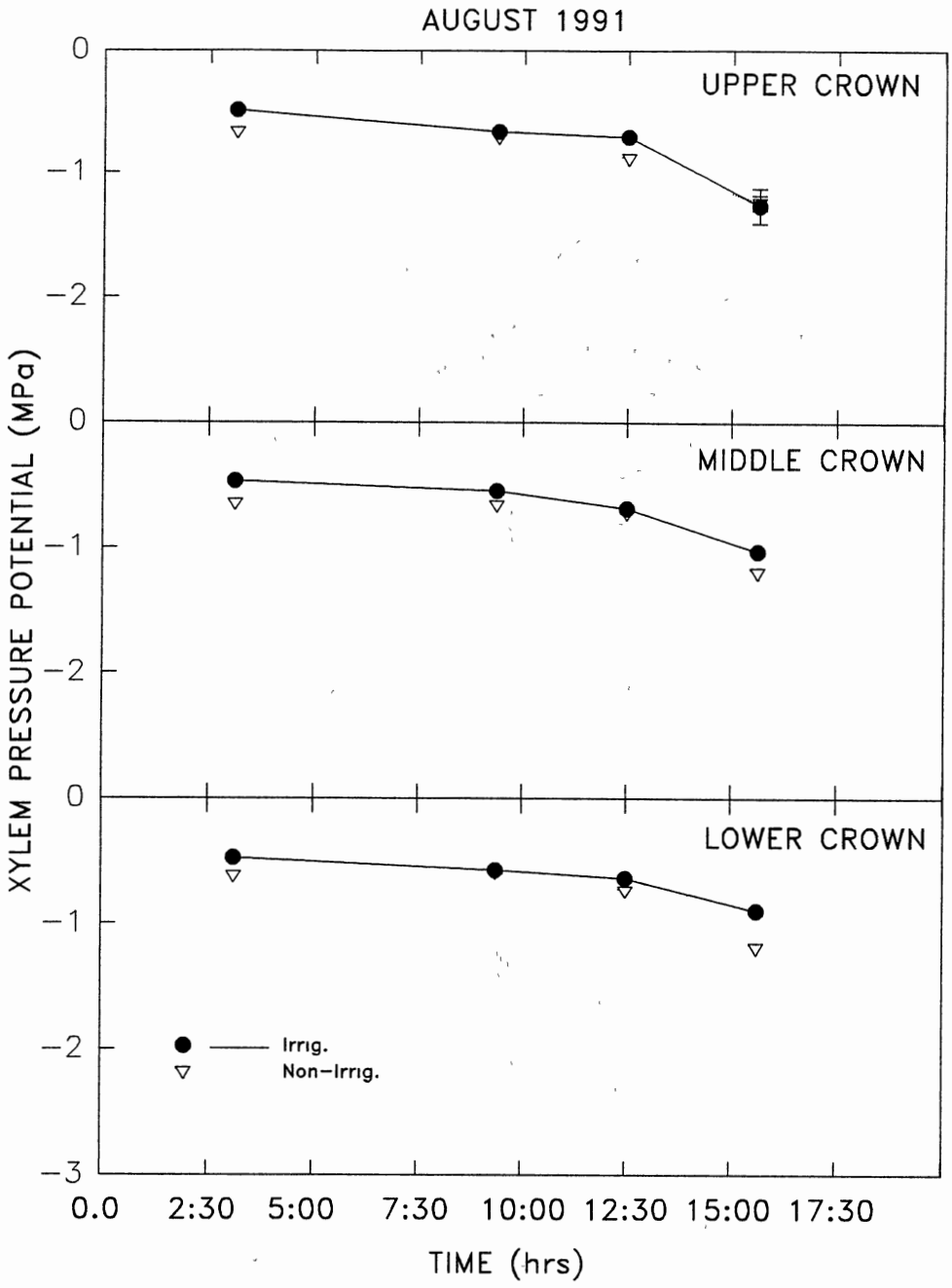

Figure 4. Diurnal patterns of xylem pressure potential for August. Each bar indicates one standard error and each point indicates the mean of three trees measured.

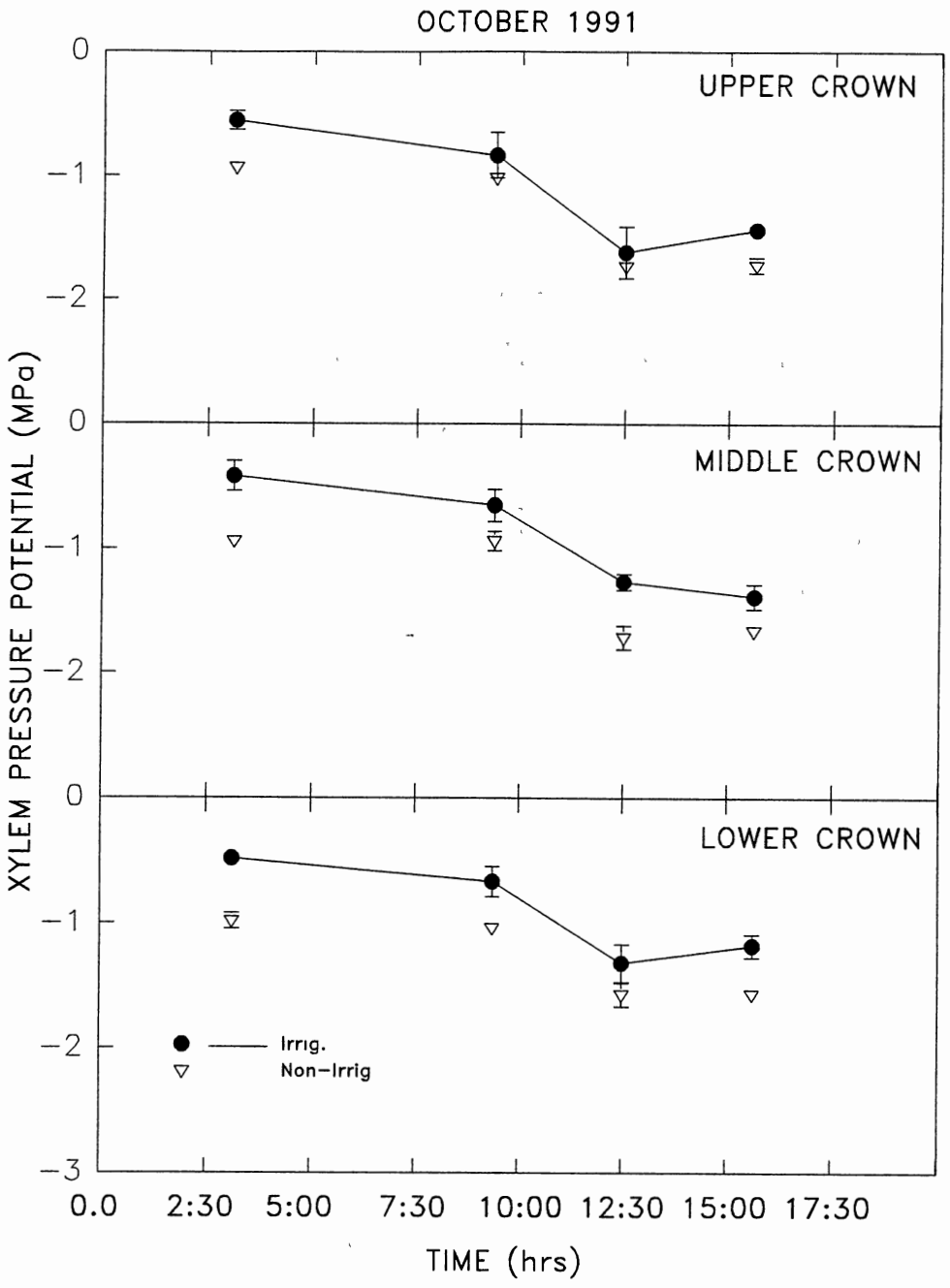

Figure 5. Diurnal patterns of xylem pressure potential for October. Each bar indicates one standard error and each point indicates the mean of three trees measured.

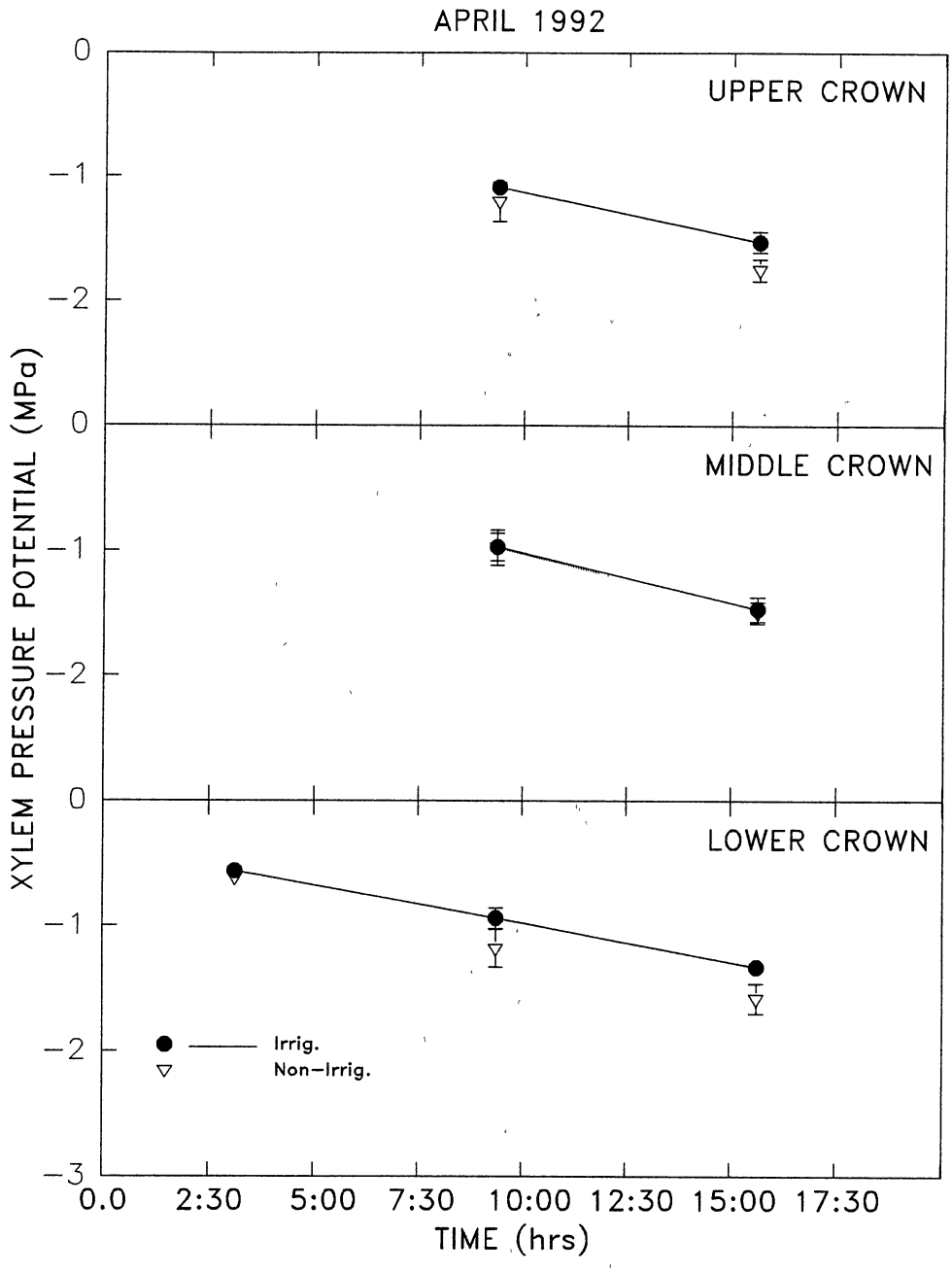

Figure 6. Diurnal patterns of xylem pressure potential for April. Each bar indicates one standard error and each point indicates the mean of three trees measured.

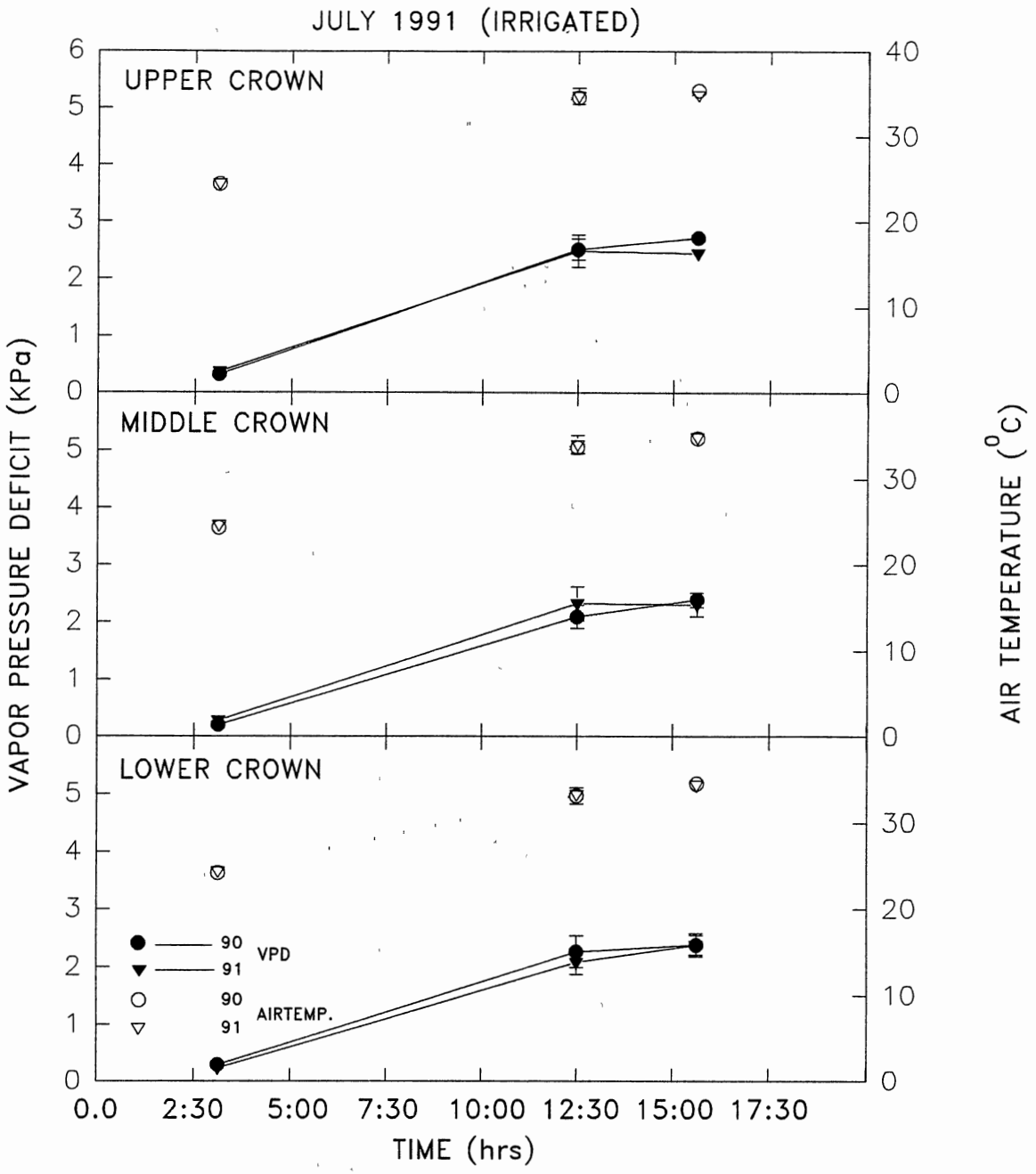

Figure 7. Diurnal patterns of air temperature and vapor pressure deficit for July. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

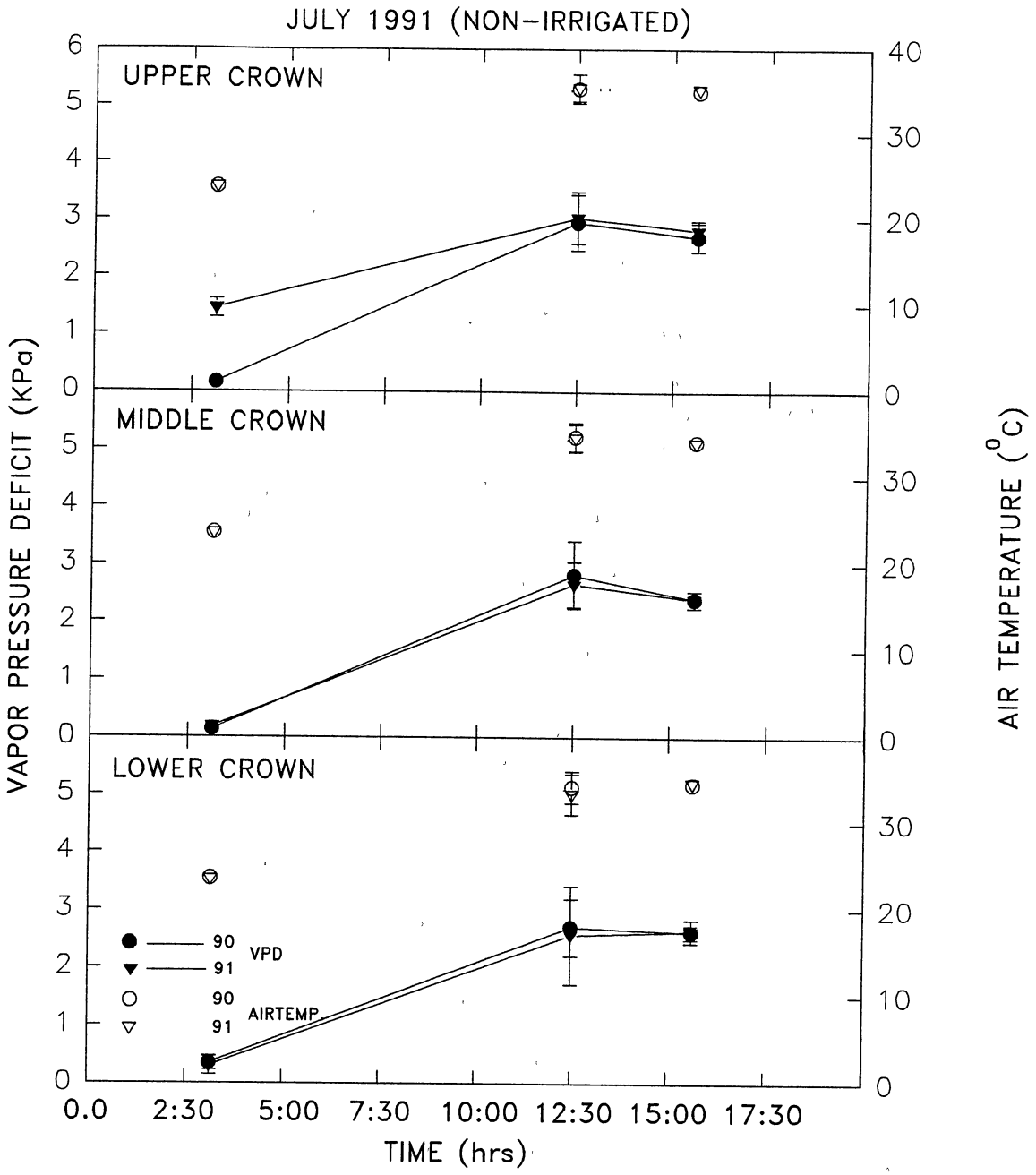

Figure 8. Diurnal patterns of air temperature and vapor pressure deficit for July. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

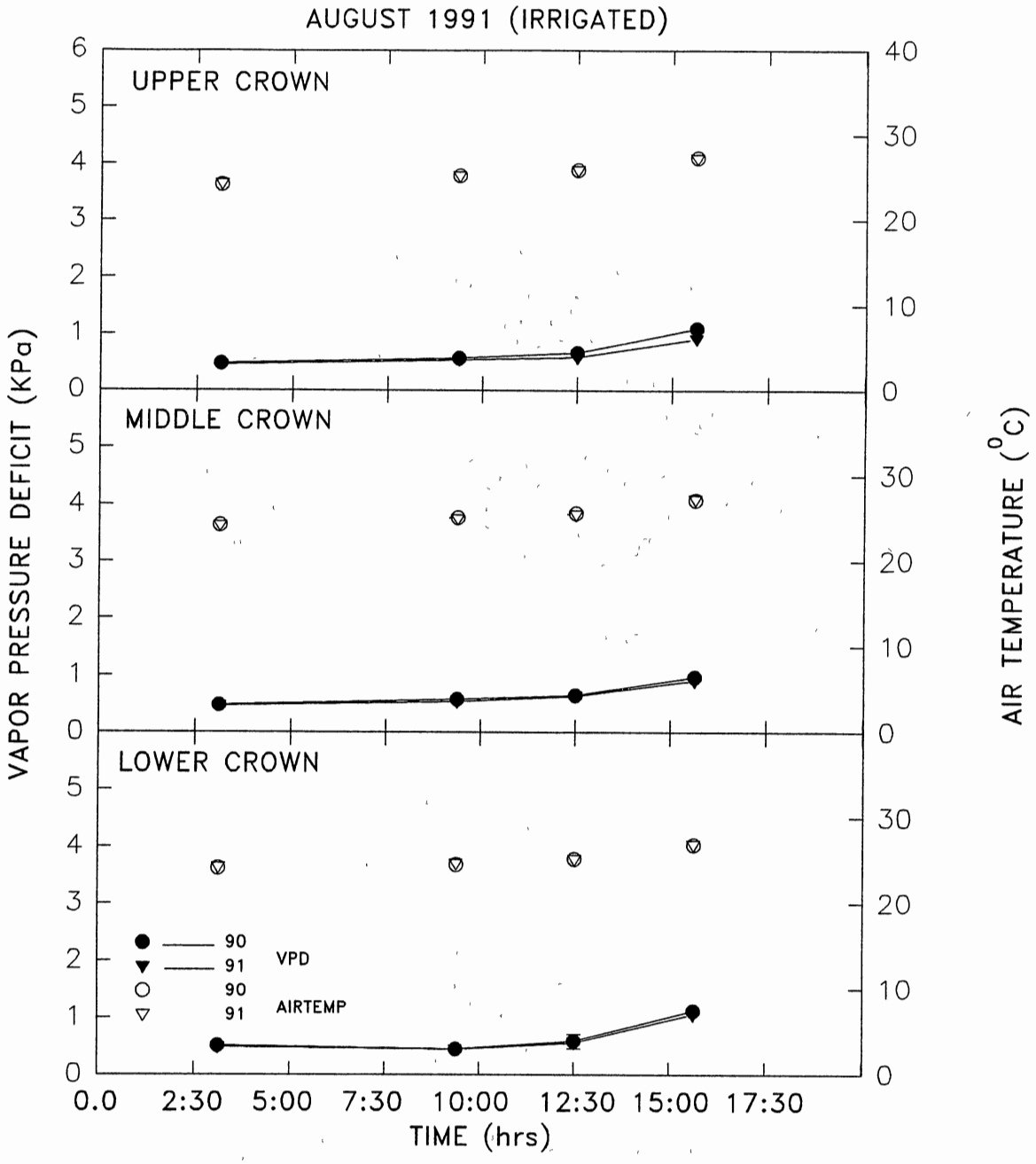

Figure 9. Diurnal patterns of air temperature and vapor pressure deficit for August. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

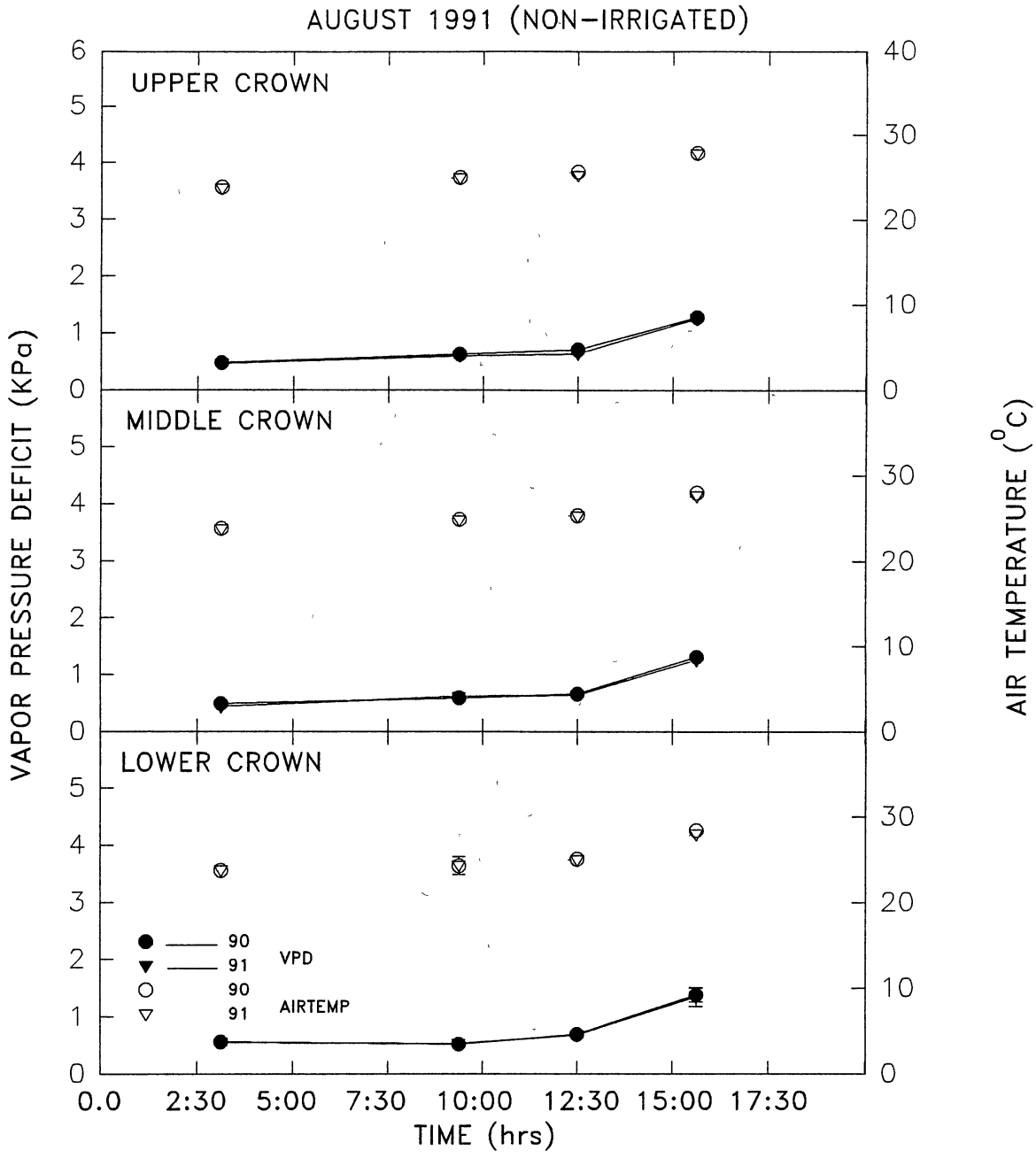

Figure 10. Diurnal patterns of air temperature and vapor pressure deficit for August. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

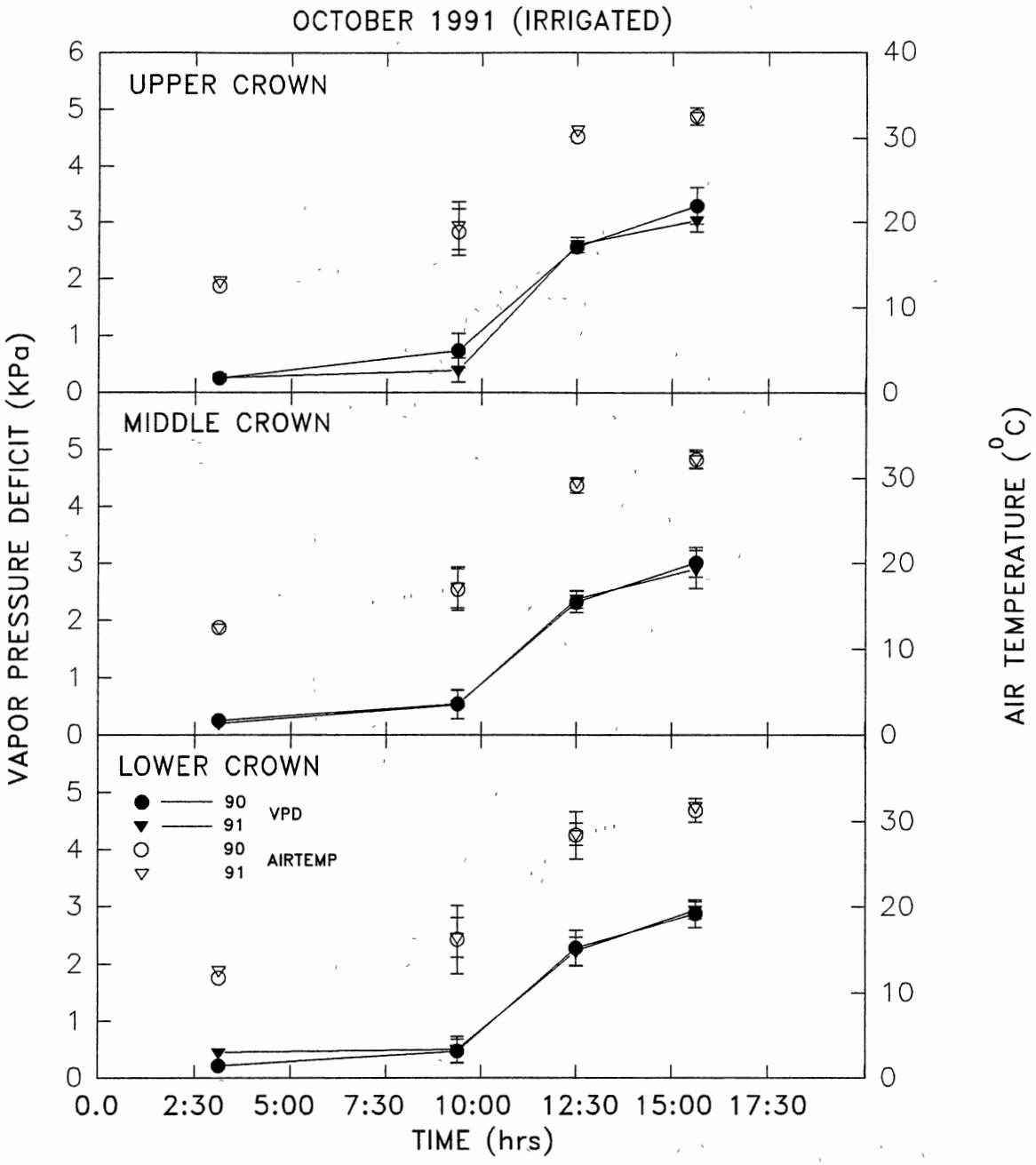

Figure 11. Diurnal patterns of air temperature and vapor pressure deficit for October. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

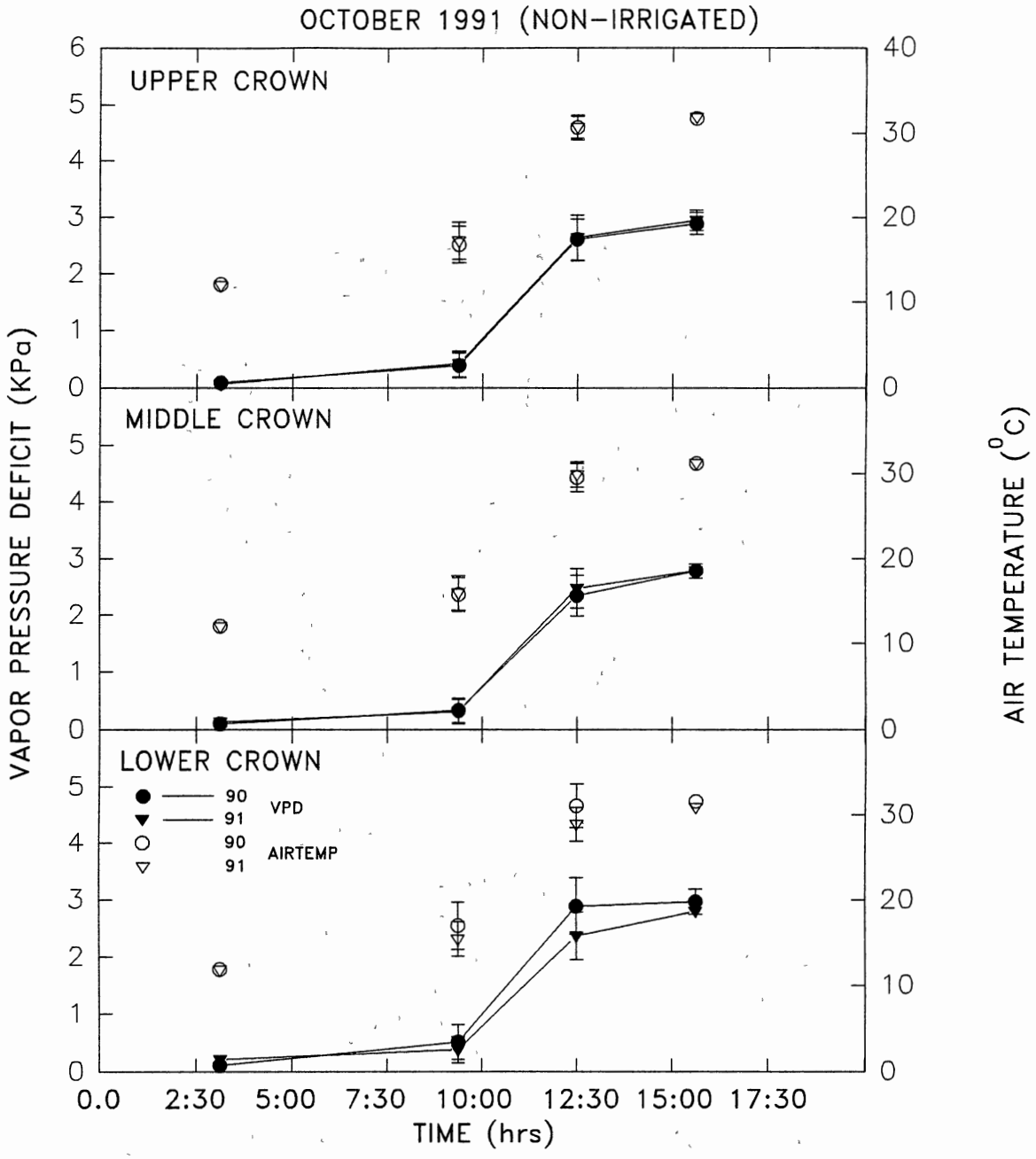

Figure 12. Diurnal patterns of air temperature and vapor pressure deficit for October. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

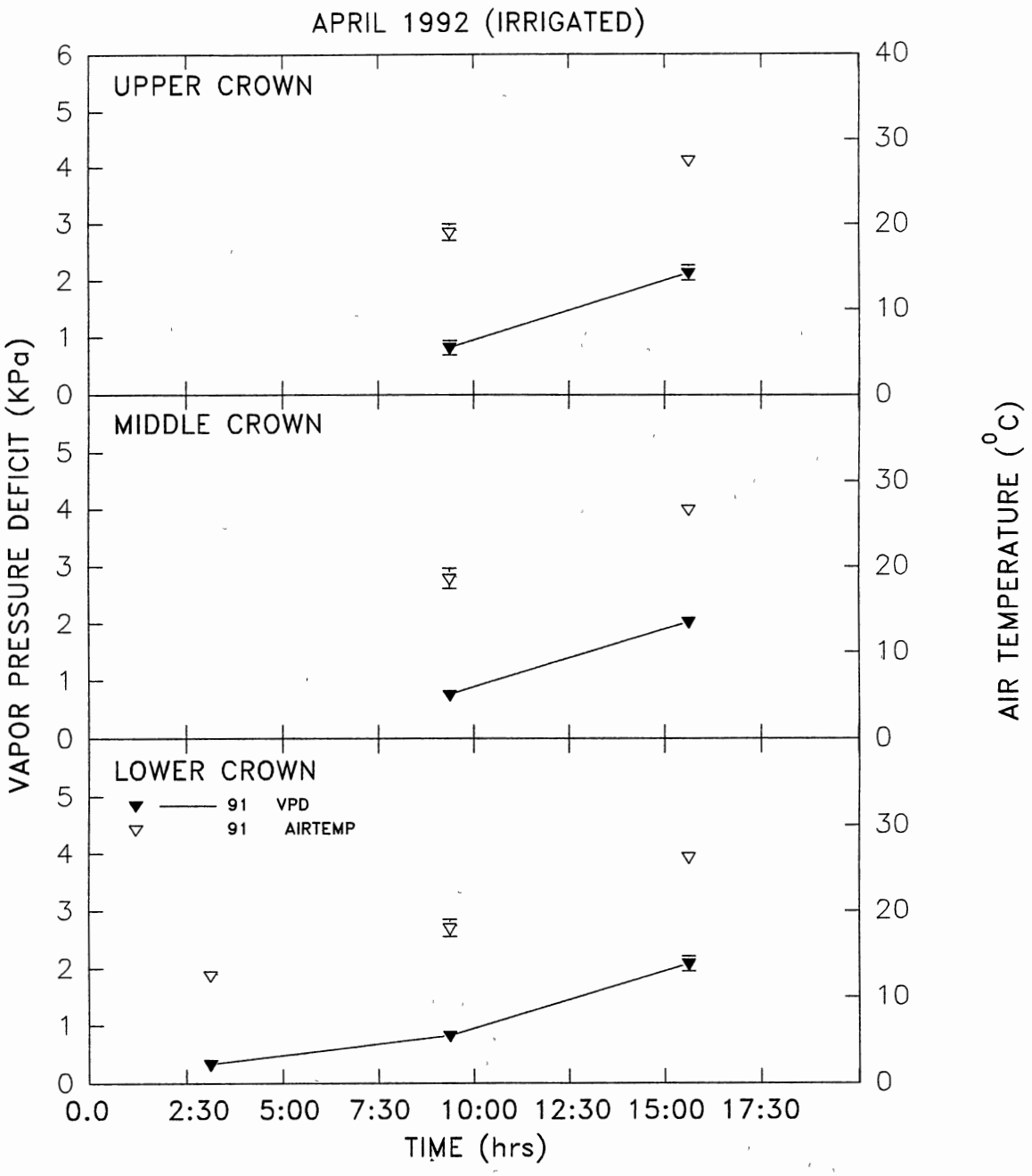

Figure 13. Diurnal patterns of air temperature and vapor pressure deficit for April. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

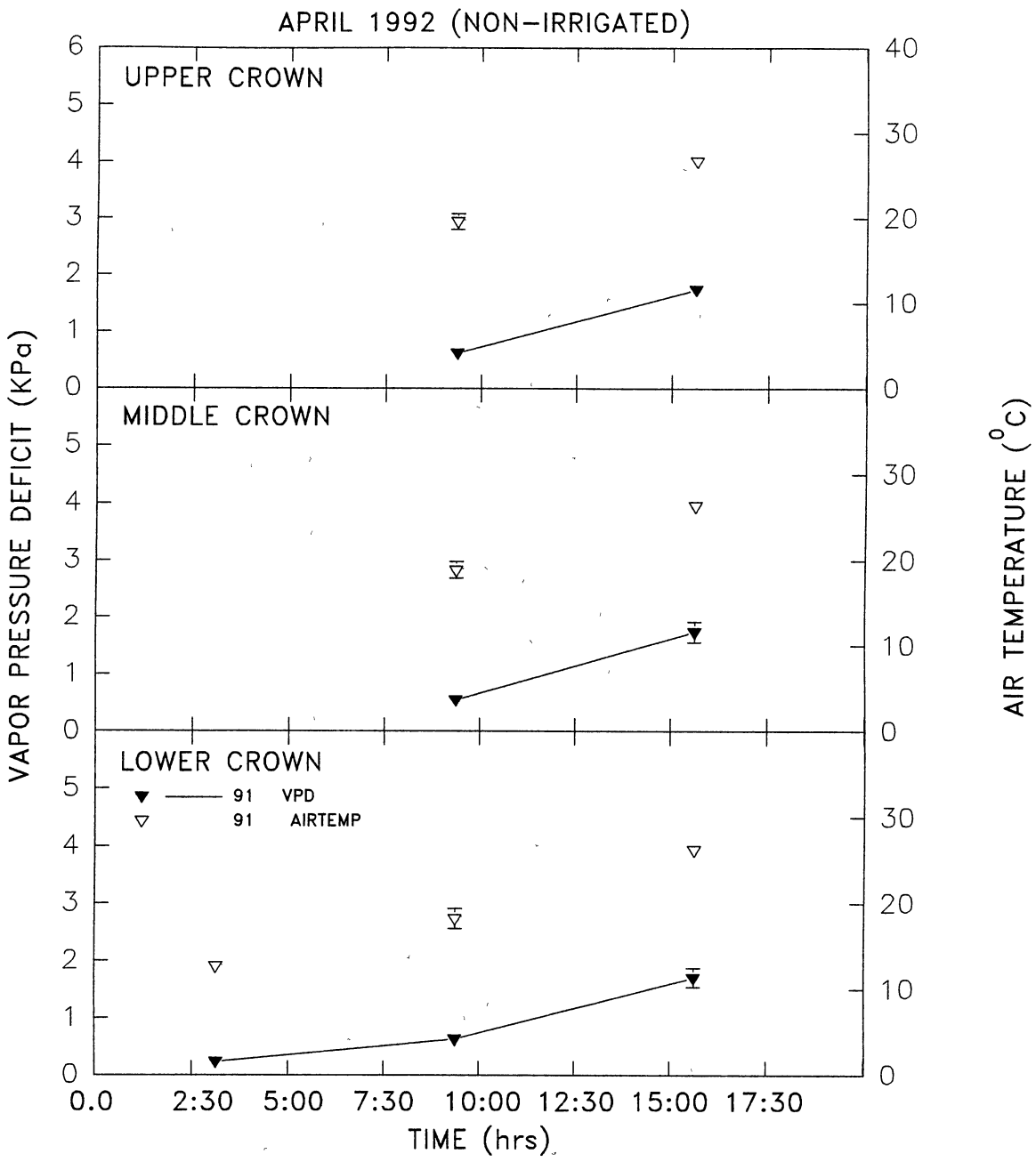

Figure 14. Diurnal patterns of air temperature and vapor pressure deficit for April. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

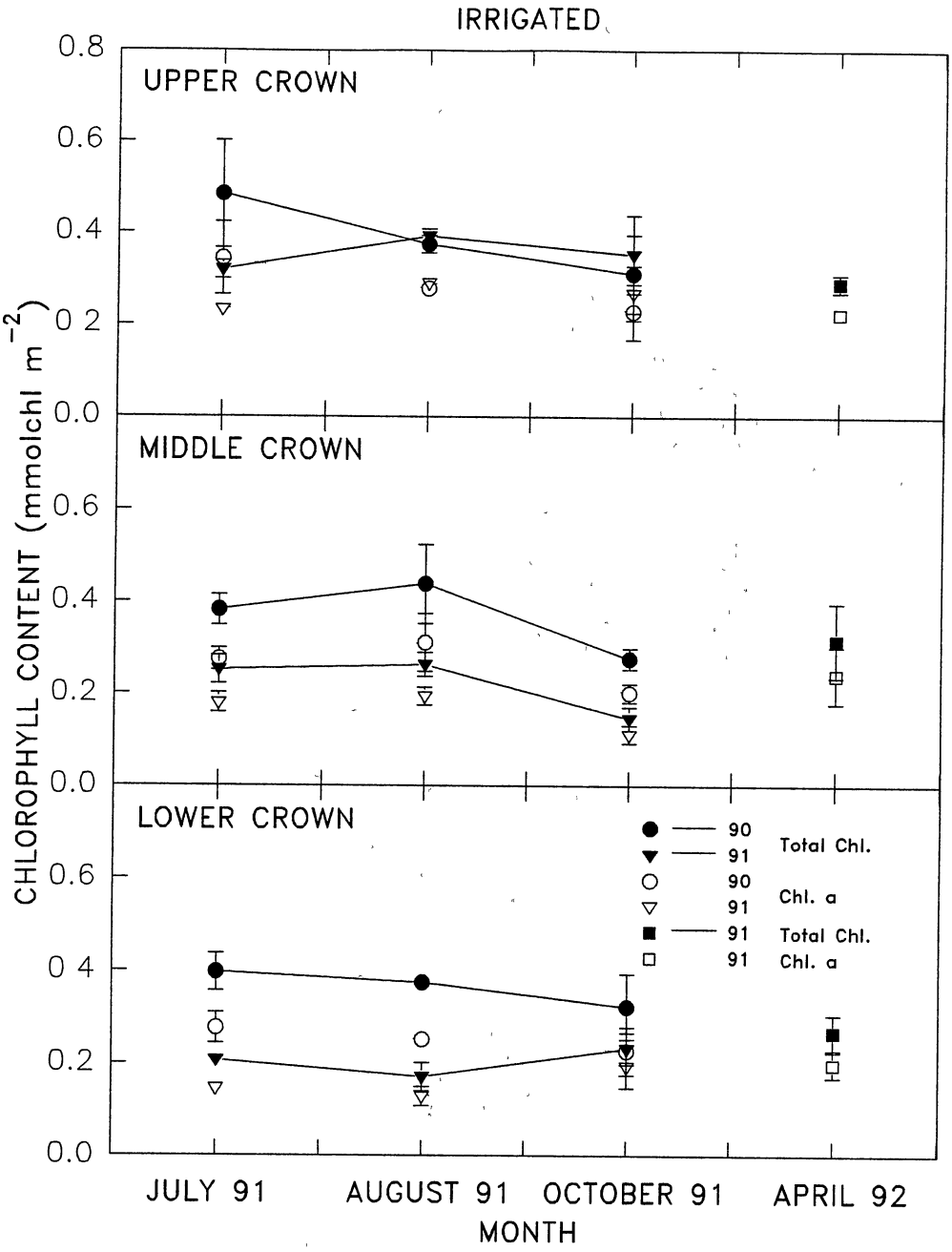

Figure 15. Seasonal patterns of total chlorophyll and chlorophyll a content. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

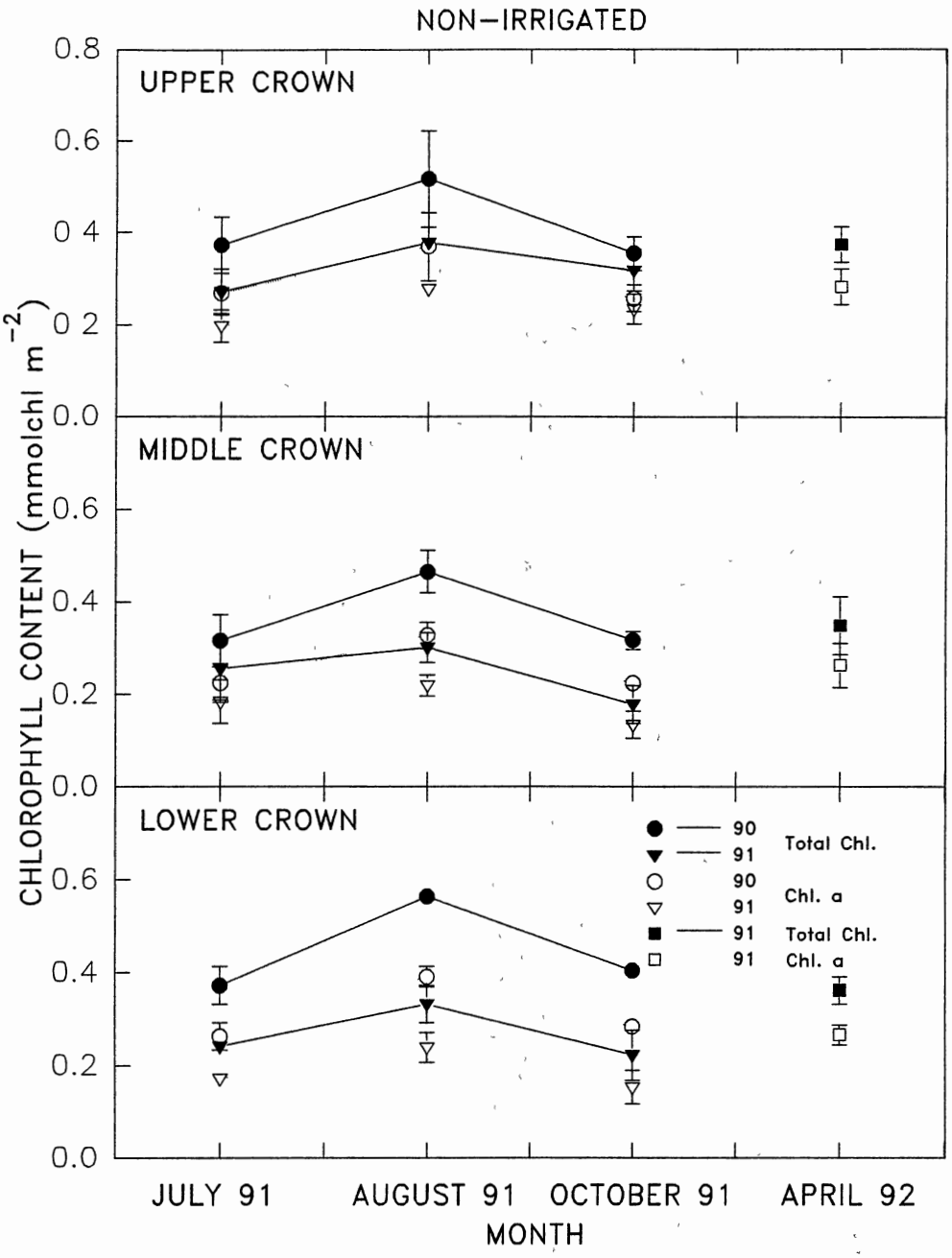

Figure 16. Seasonal patterns of total chlorophyll and chlorophyll a content. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

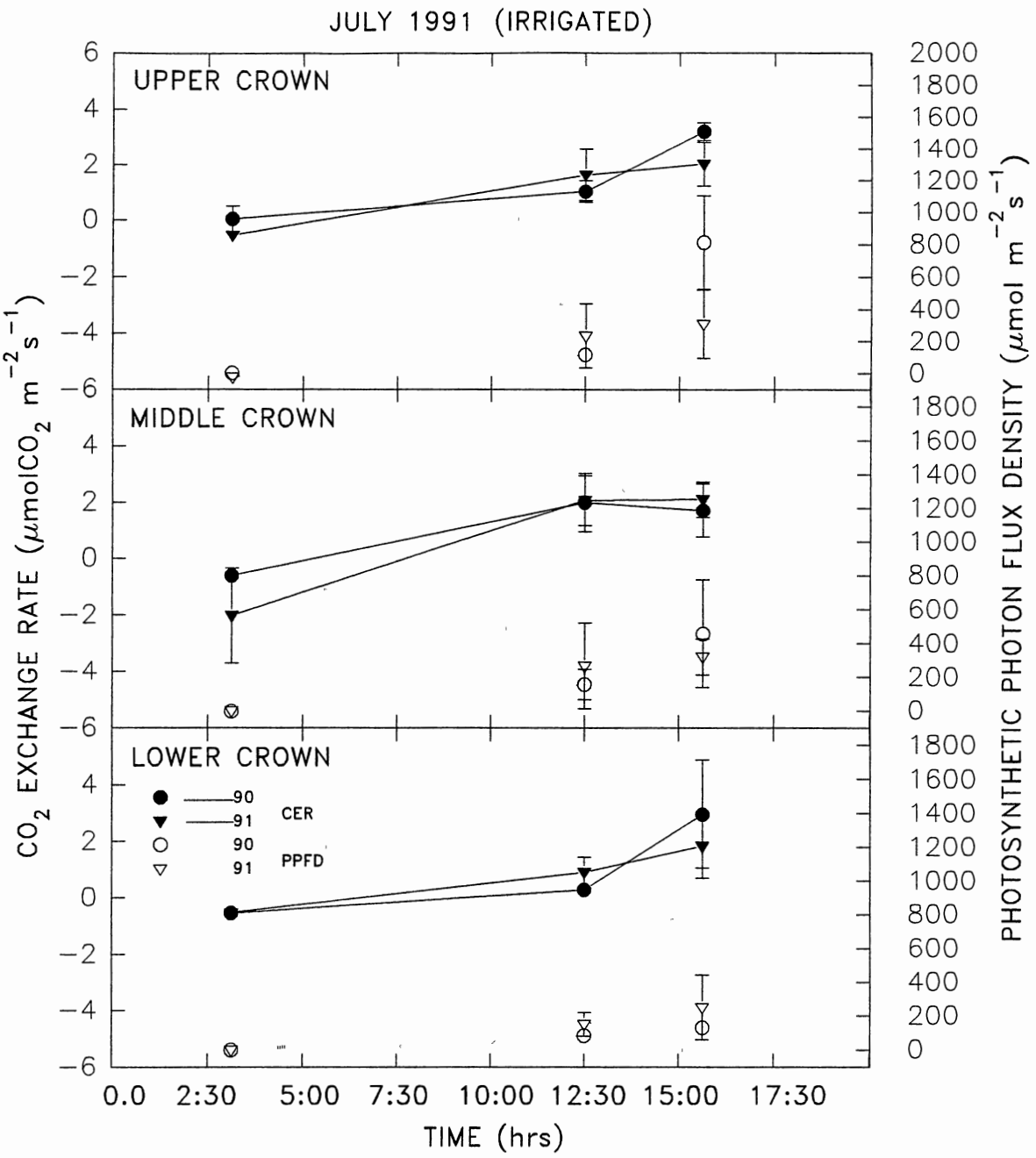

Figure 17. Diurnal patterns of carbon exchange rate and photosynthetic photon flux density for July. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

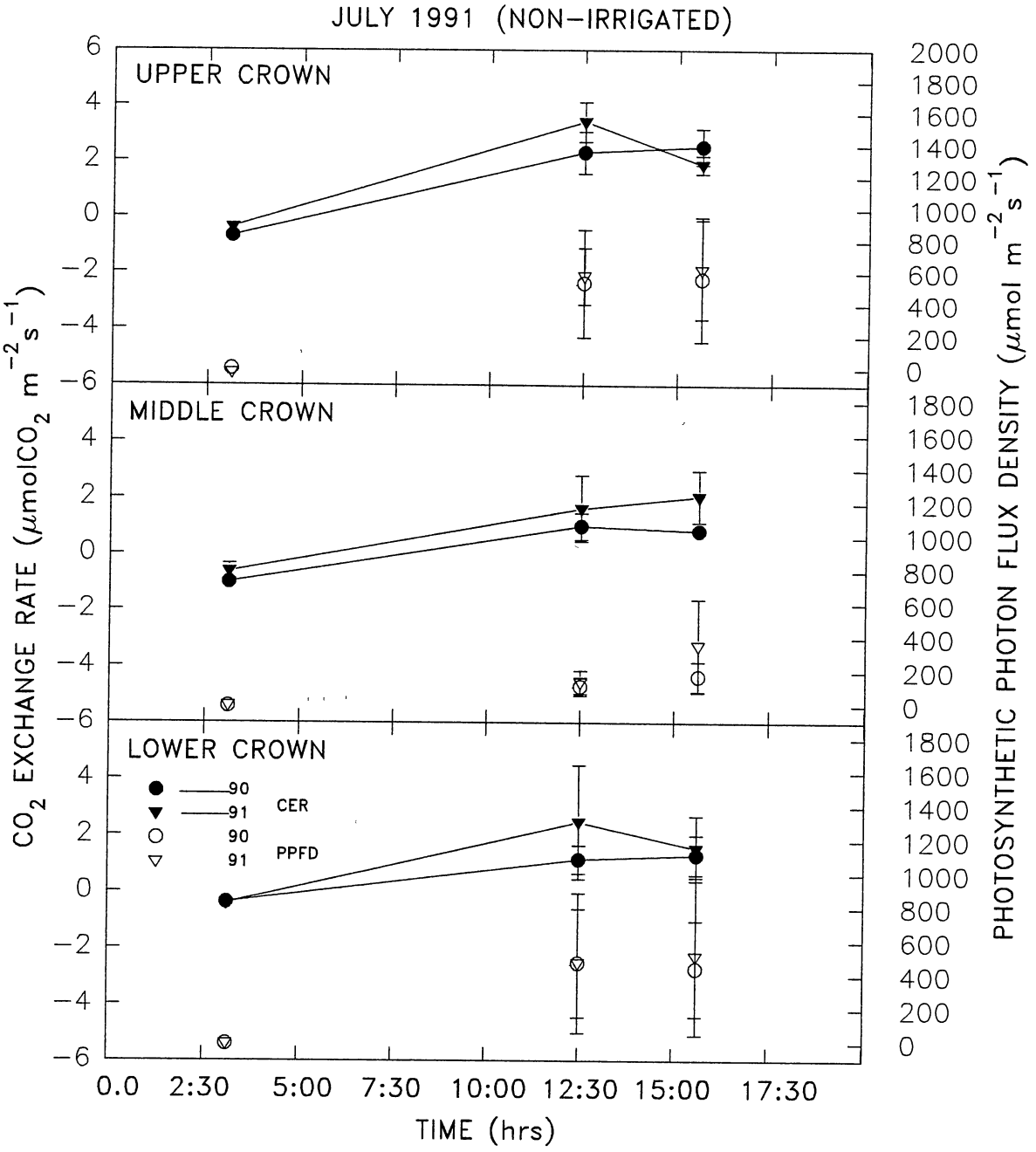

Figure 18. Diurnal patterns of carbon exchange rate and photosynthetic photon flux density for July. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

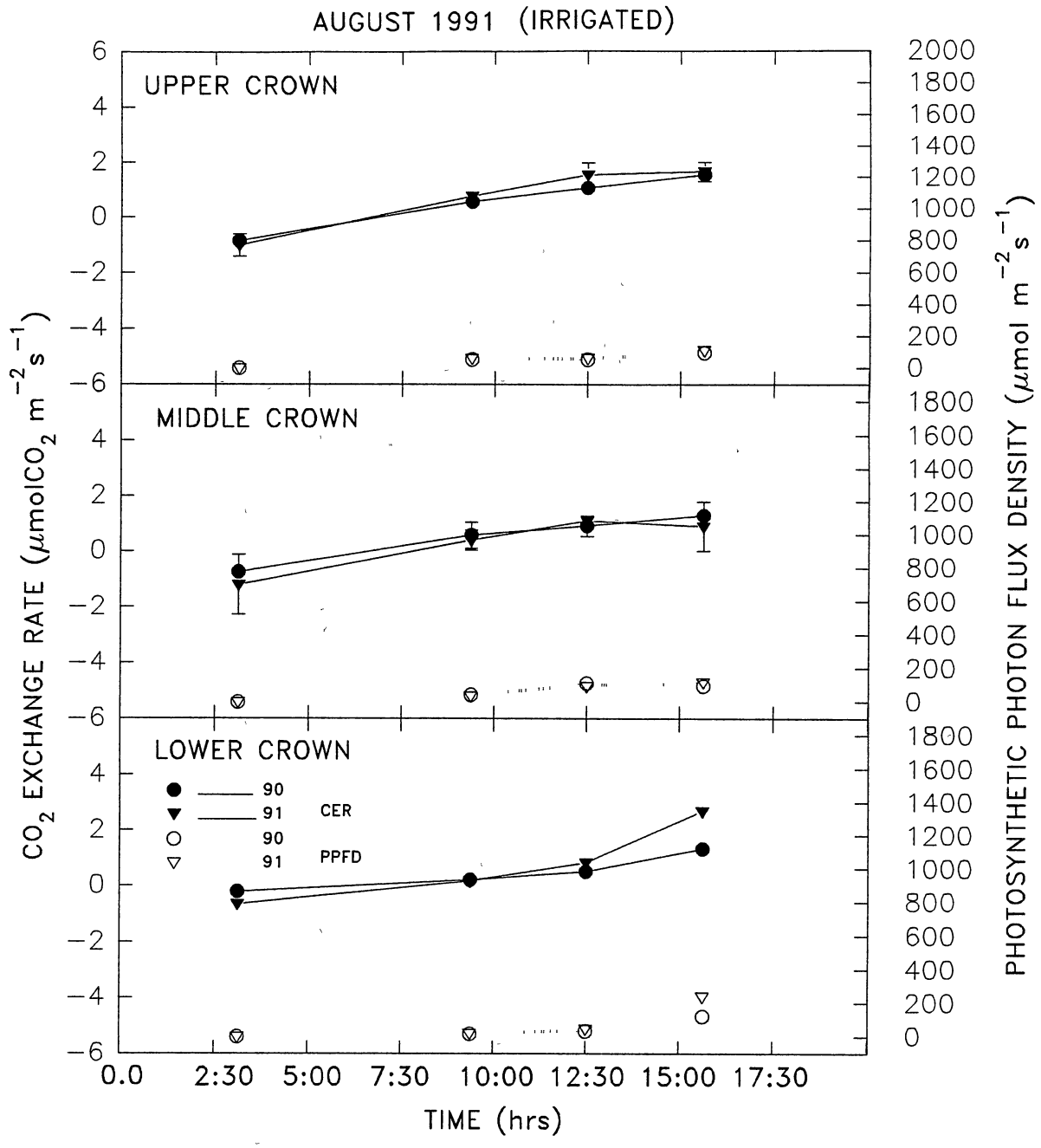

Figure 19. Diurnal patterns of carbon exchange rate and photosynthetic photon flux density for August. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

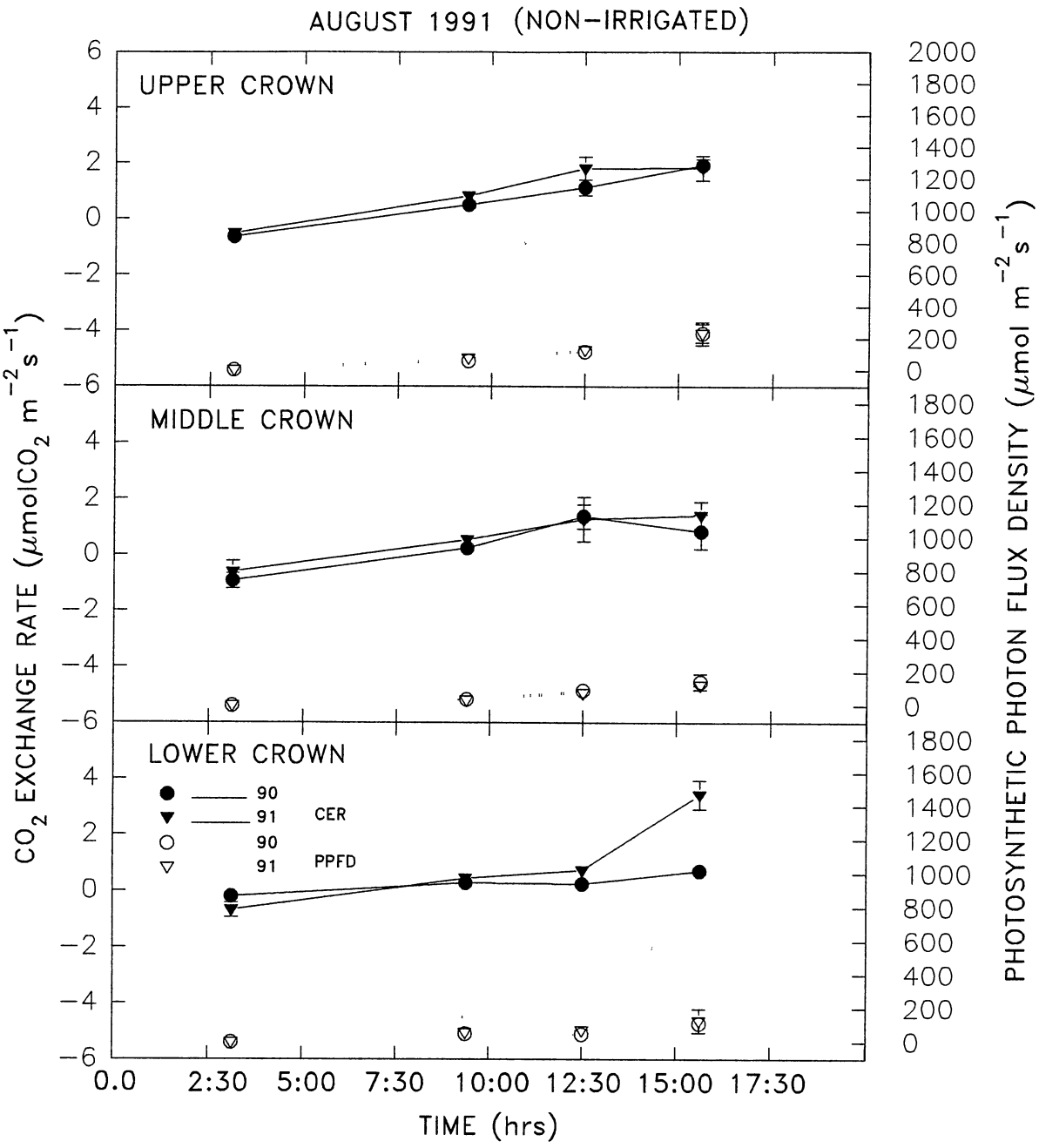

Figure 20. Diurnal patterns of carbon exchange rate and photosynthetic photon flux density for August. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

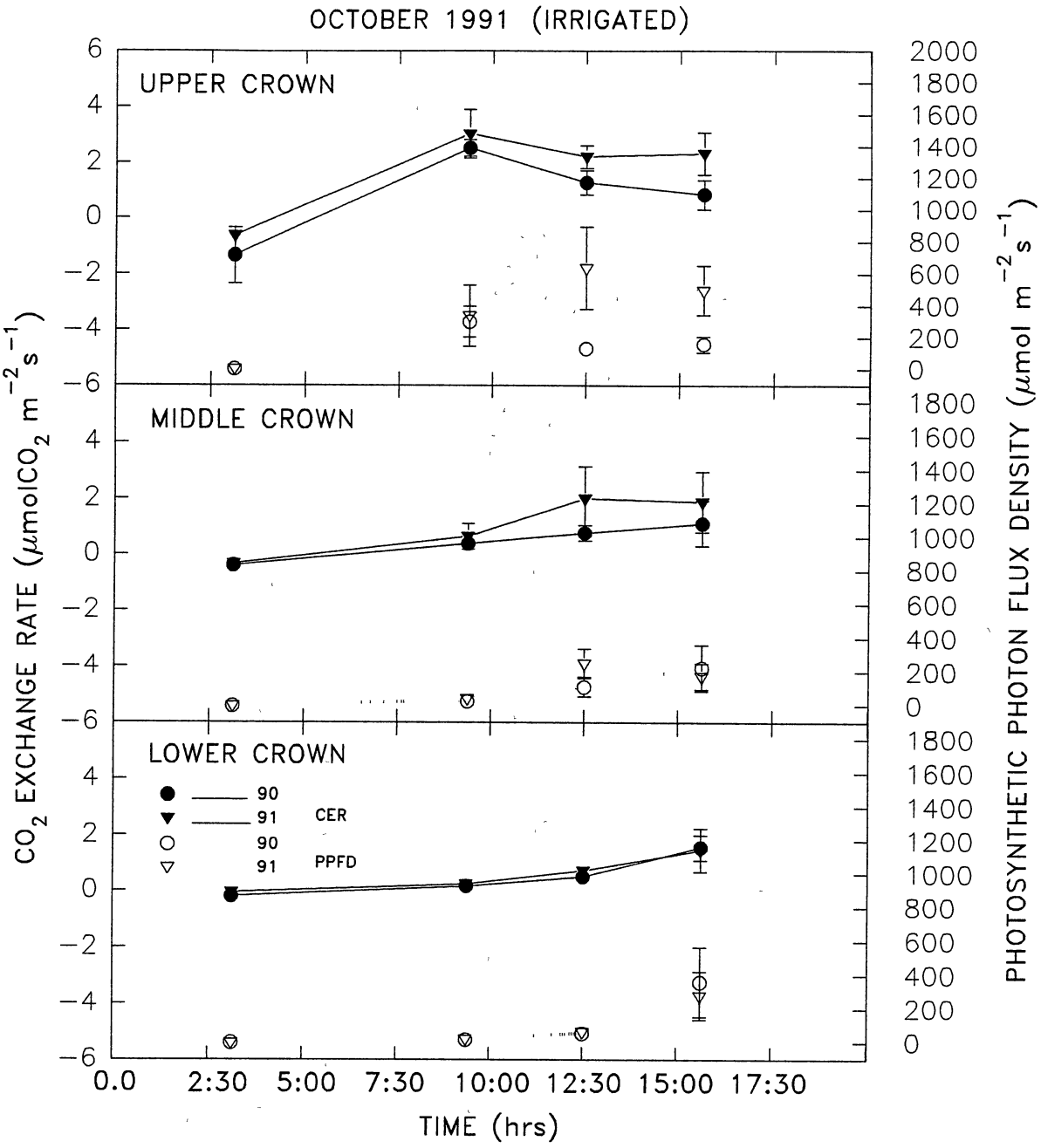

Figure 21. Diurnal patterns of carbon exchange rate and photosynthetic photon flux density for October. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

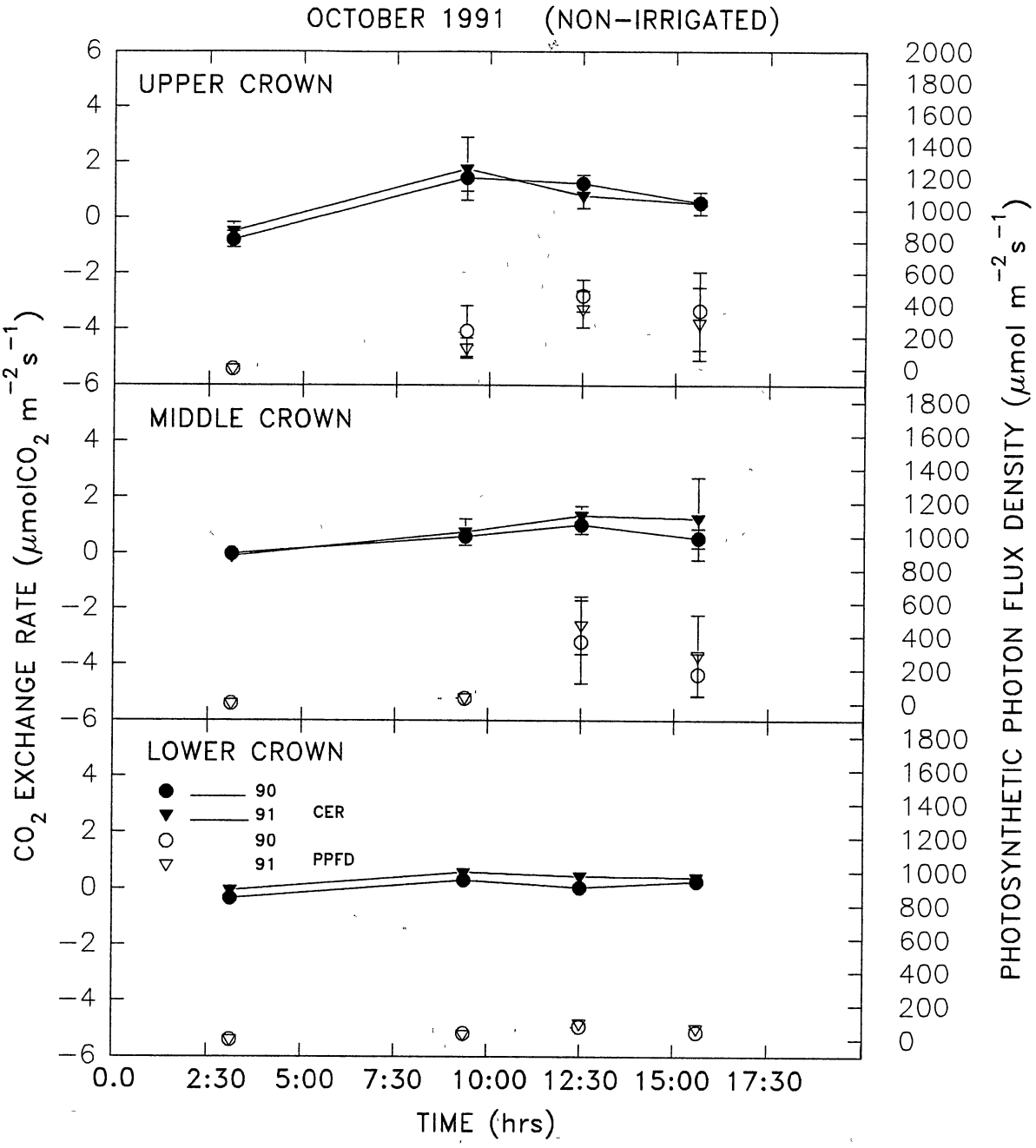

Figure 22. Diurnal patterns of carbon exchange rate and photosynthetic photon flux density for October. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

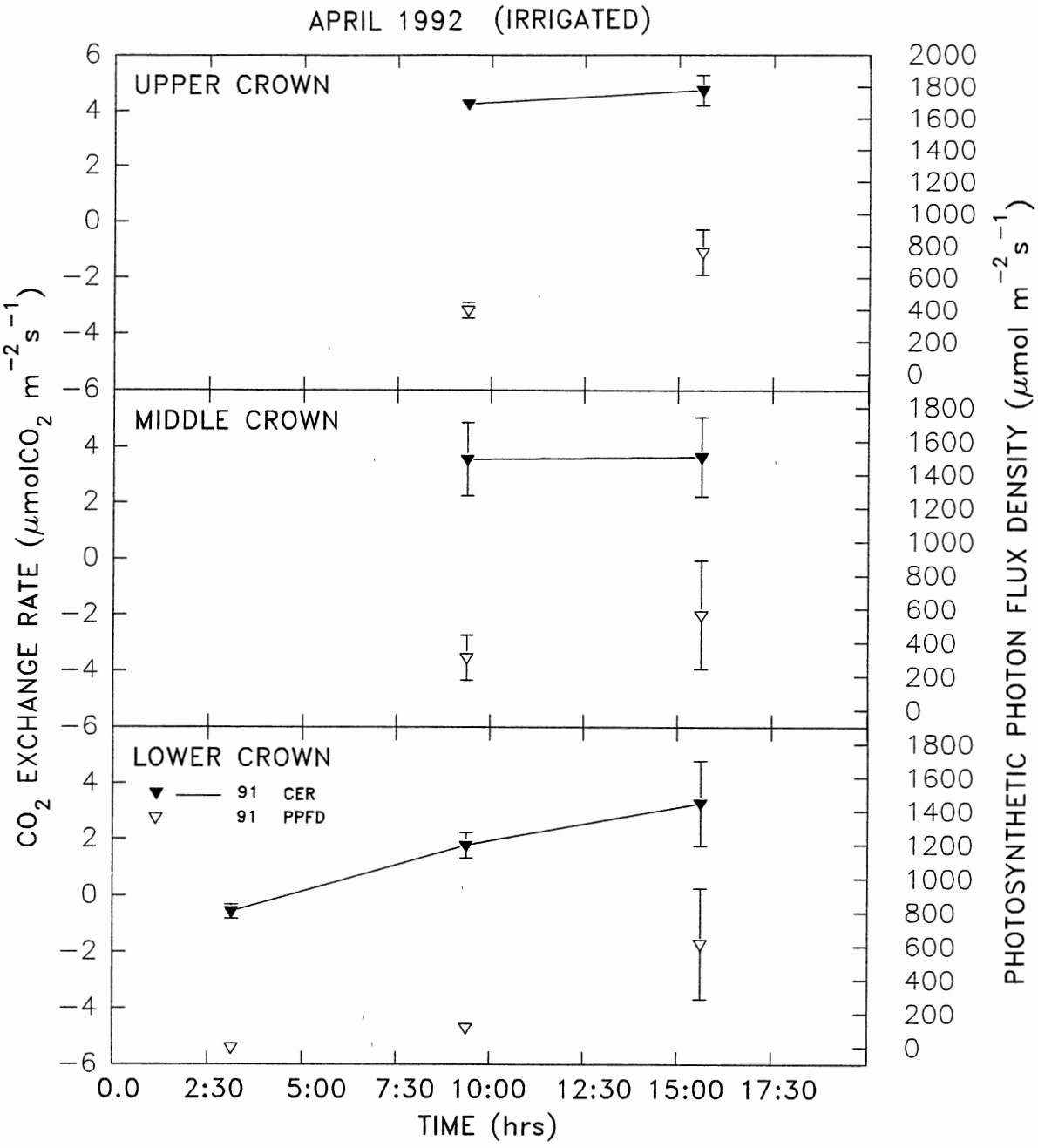

Figure 23. Diurnal patterns of carbon exchange rate and photosynthetic photon flux density for April. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

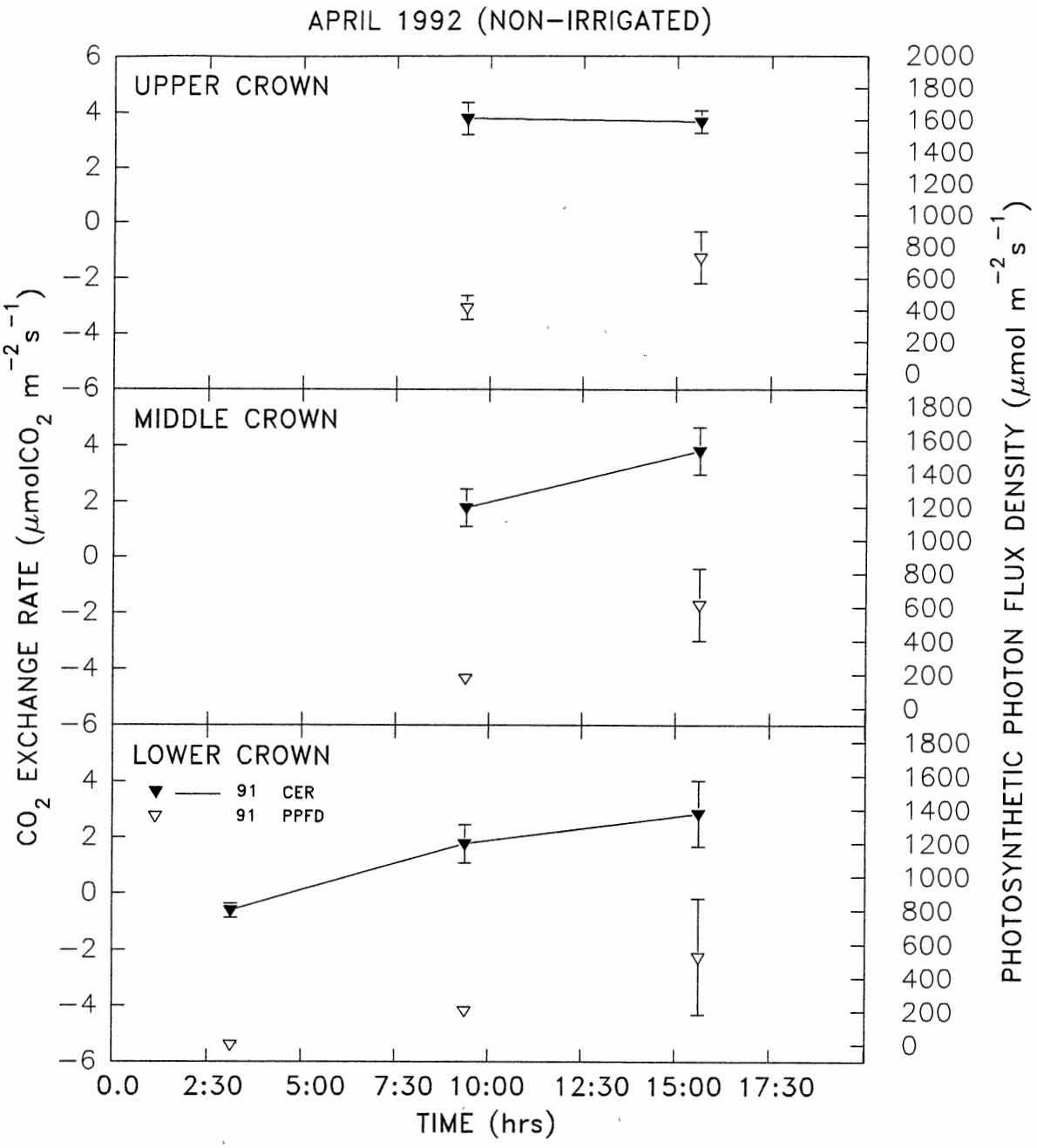

Figure 24. Diurnal patterns of carbon exchange rate and photosynthetic photon flux density for April. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

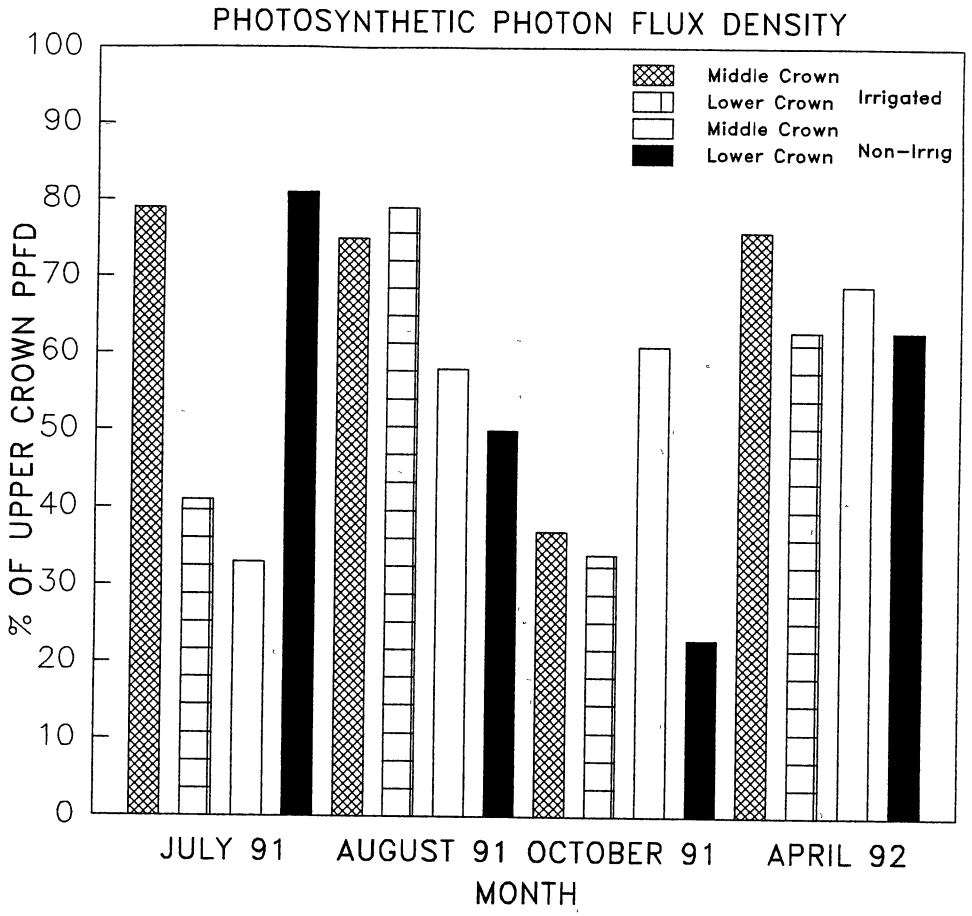

Figure 25. Photosynthetic photon flux density (PPFD) averaged over age-flush class of middle and lower crown positions based on the percent of PPFD recorded in the upper crown by month in both the irrigated and non-irrigated plots.

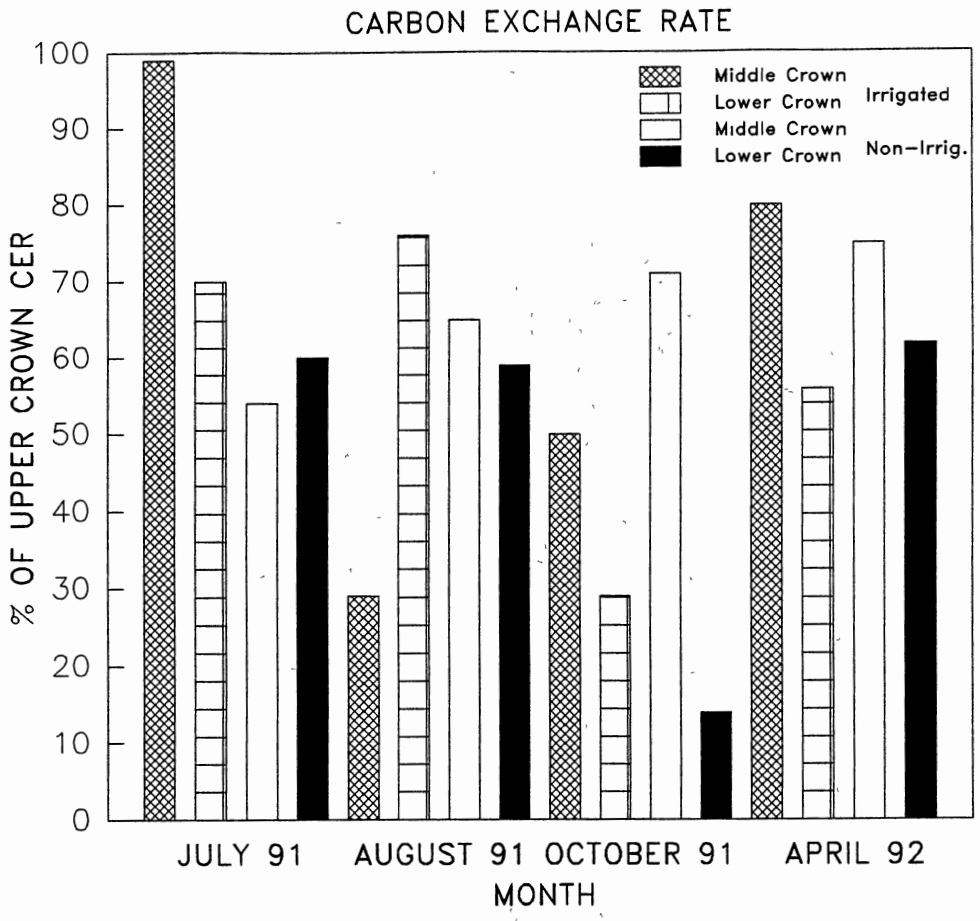

Figure 26. Carbon exchange rate (CER) averaged over age-flush class of middle and lower crown positions based on the percent of CER recorded in the upper crown by month in both the irrigated and non-irrigated plots.

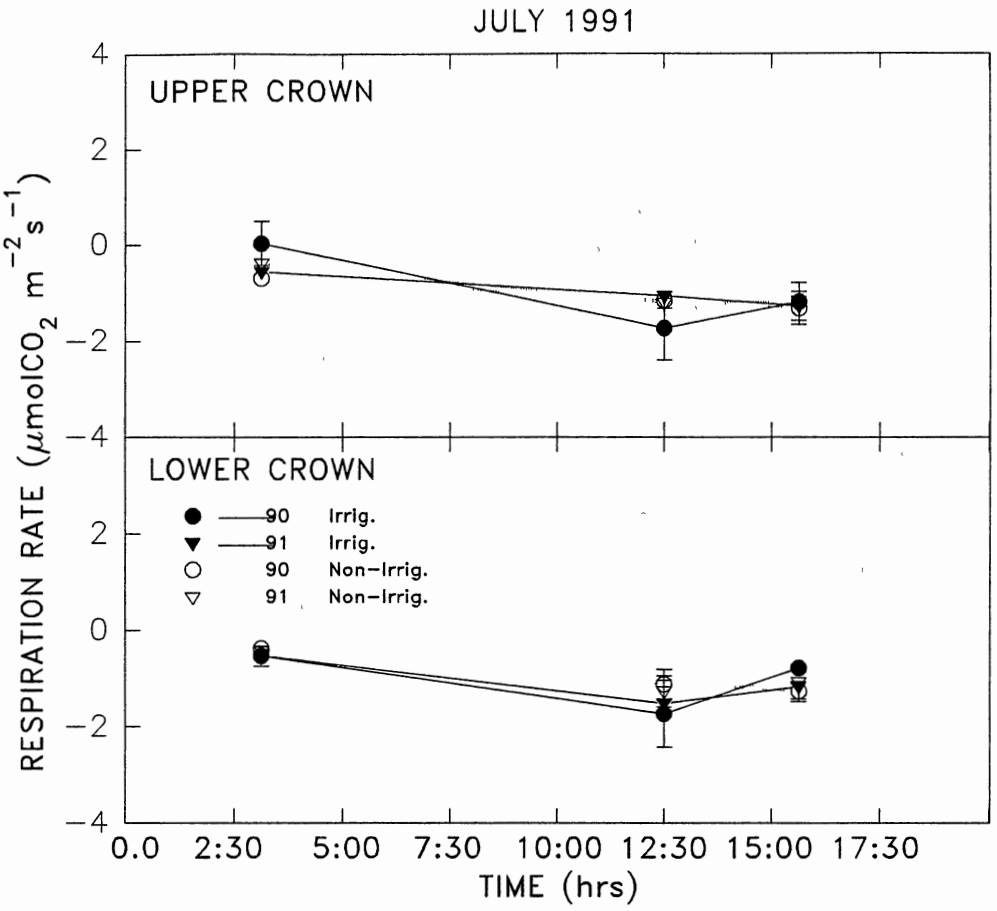

Figure 27. Diurnal patterns of respiration for July. Each bar indicates one standard error and each point indicates the mean of three trees measured.

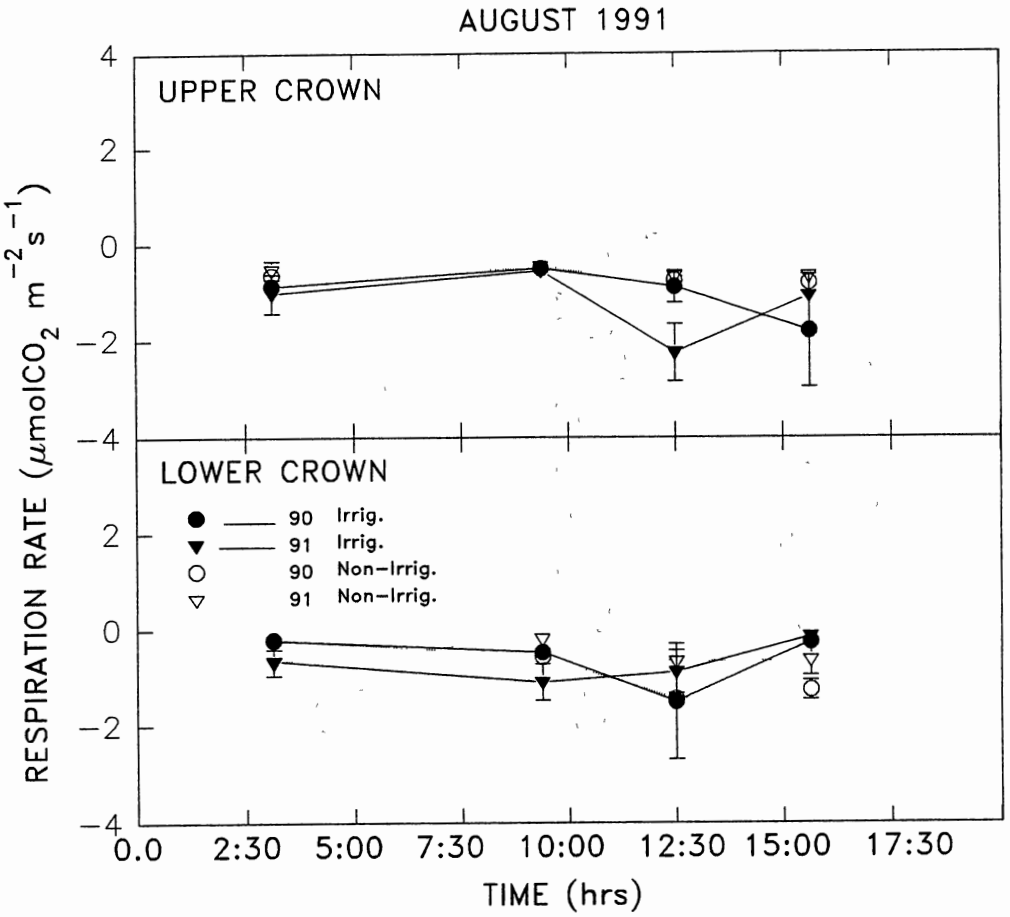

Figure 28. Diurnal patterns of respiration for August. Each bar indicates one standard error and each point indicates the mean of three trees measured.

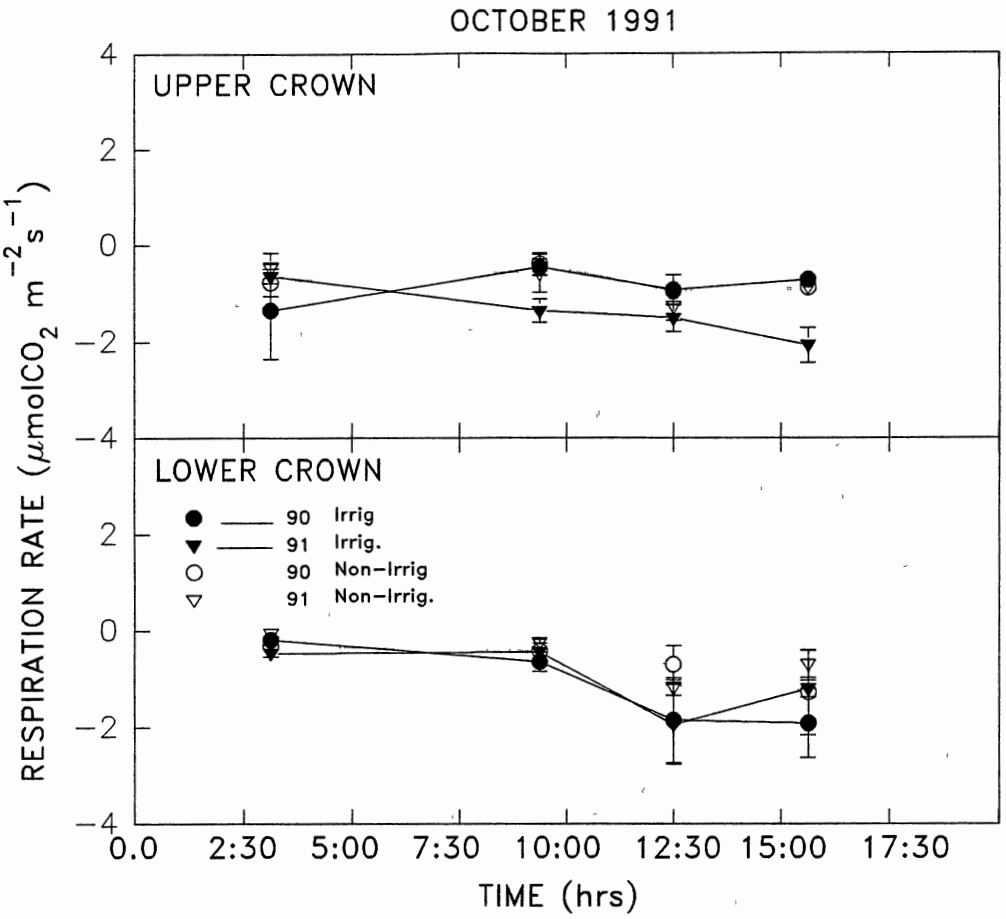

Figure 29. Diurnal patterns of respiration for October. Each bar indicates one standard error and each point indicates the mean of three trees measured.

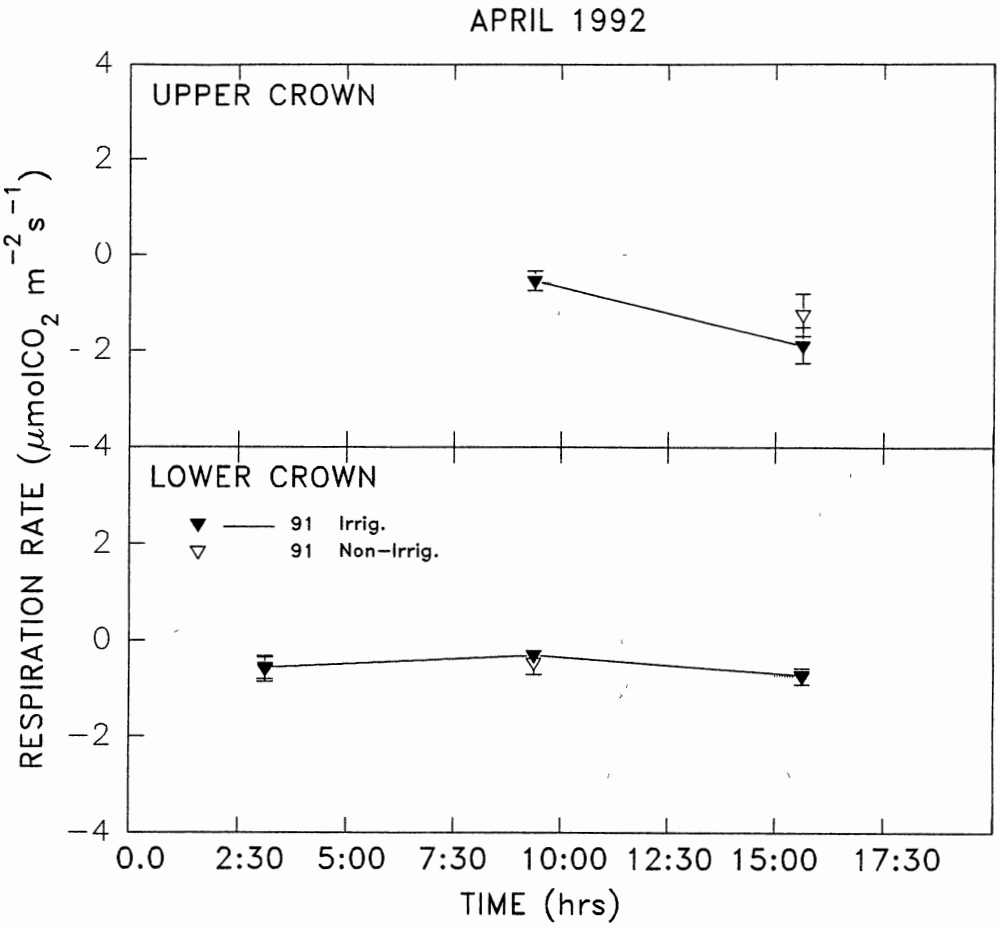

Figure 30. Diurnal patterns of respiration for April. Each bar indicates one standard error and each point indicates the mean of three trees measured.

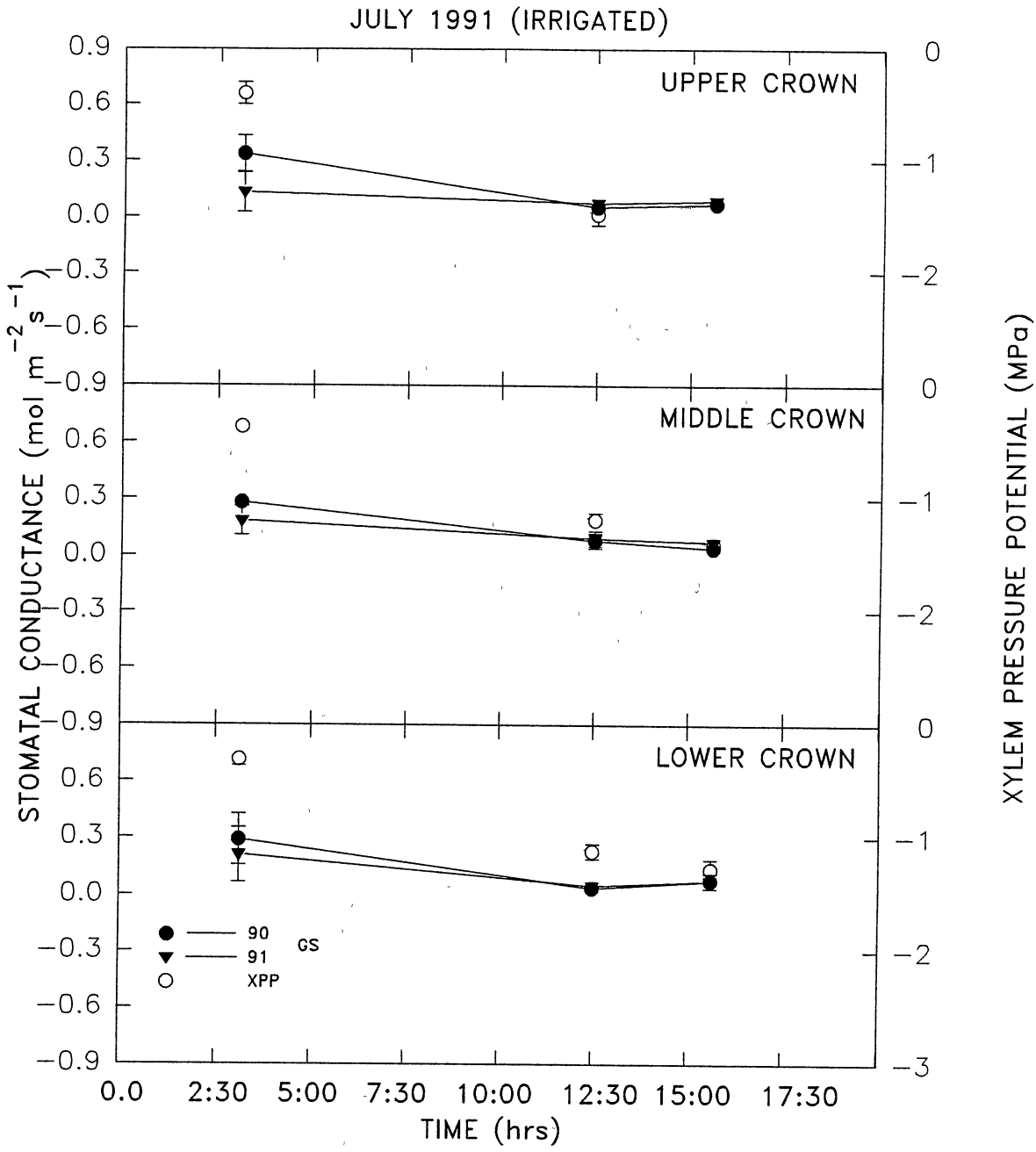

Figure 31. Diurnal patterns of stomatal conductance and xylem pressure potential for July. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

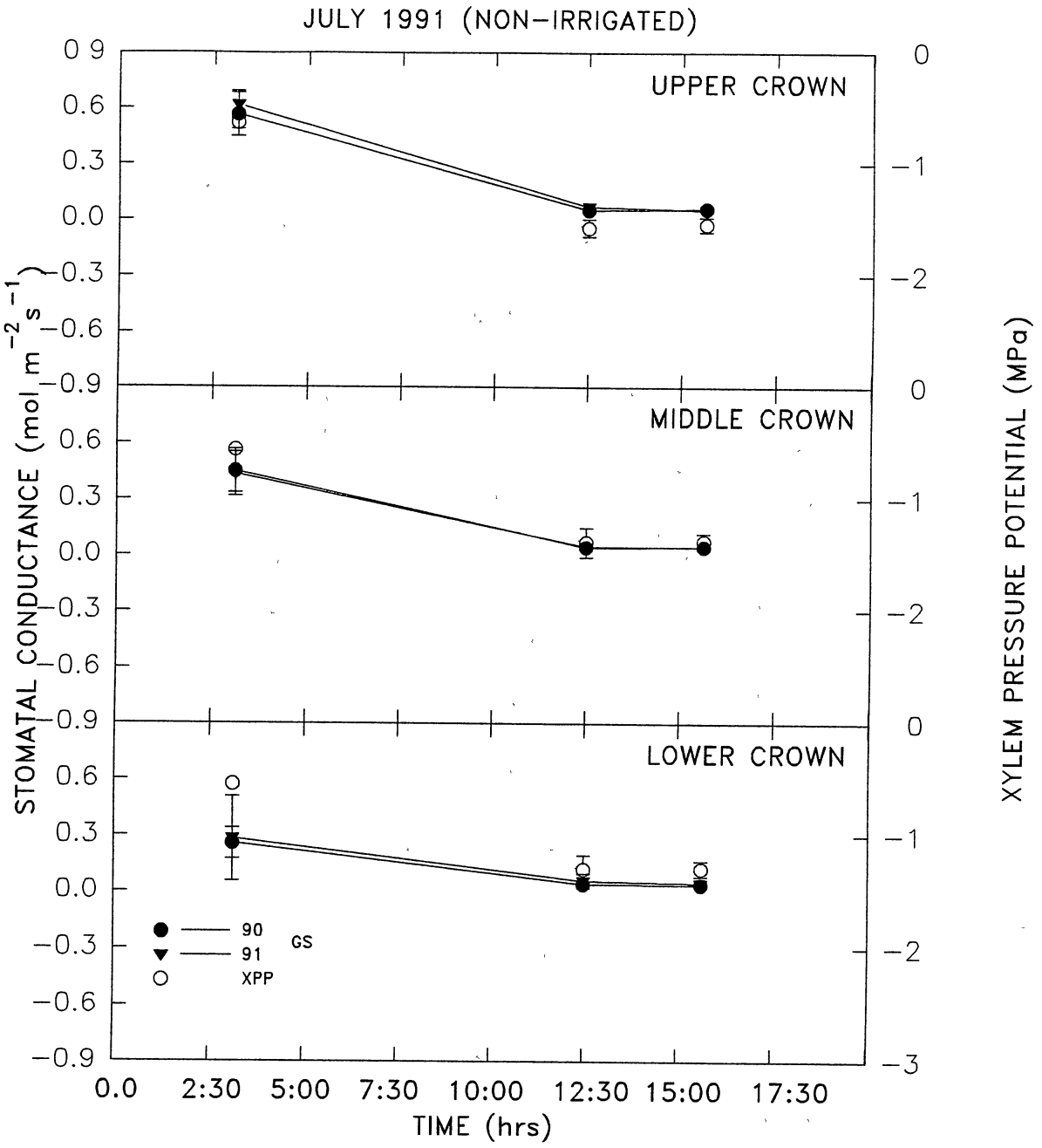

Figure 32. Diurnal patterns of stomatal conductance and xylem pressure potential for July. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

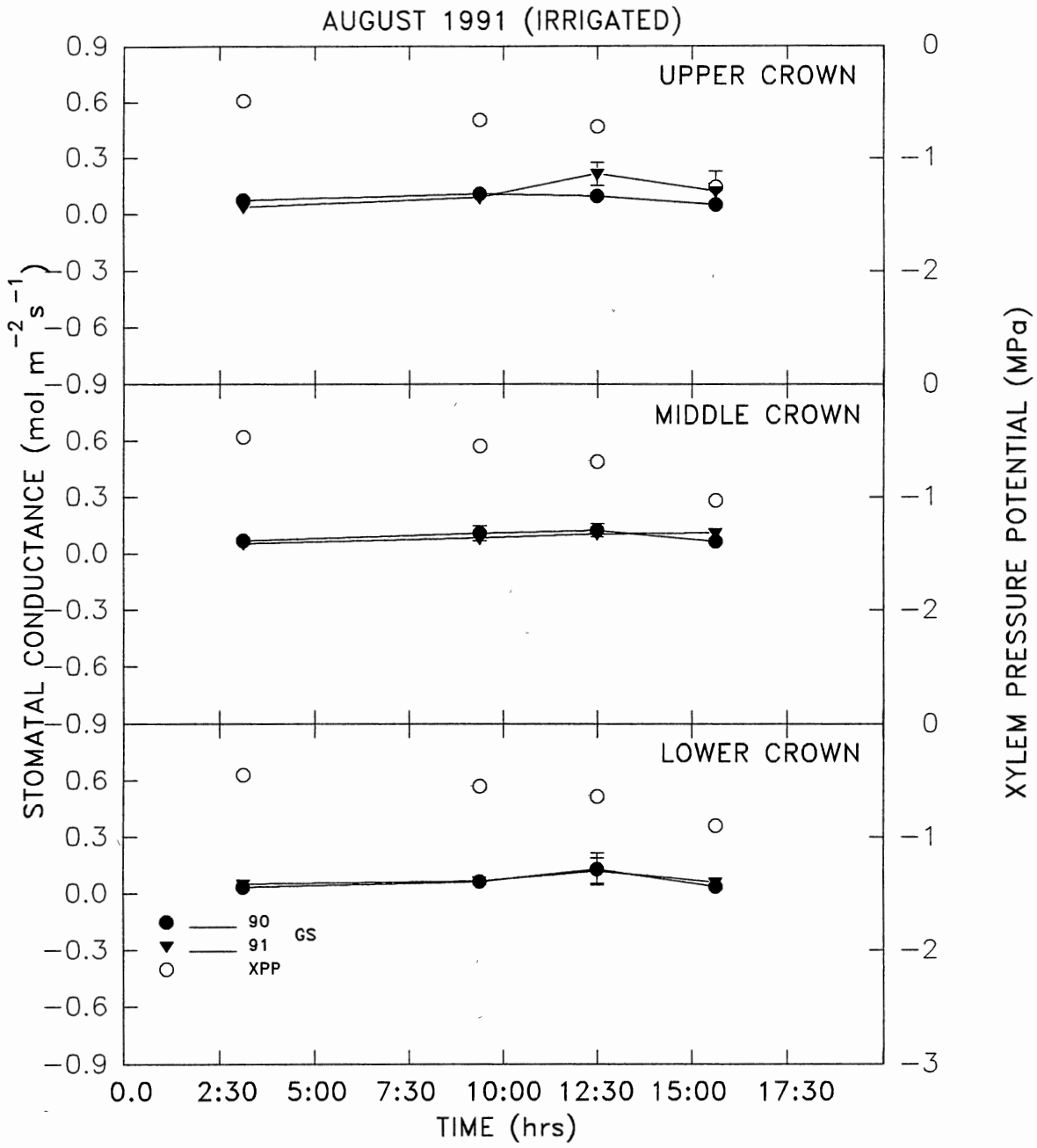

Figure 33. Diurnal patterns of stomatal conductance and xylem pressure potential for August. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

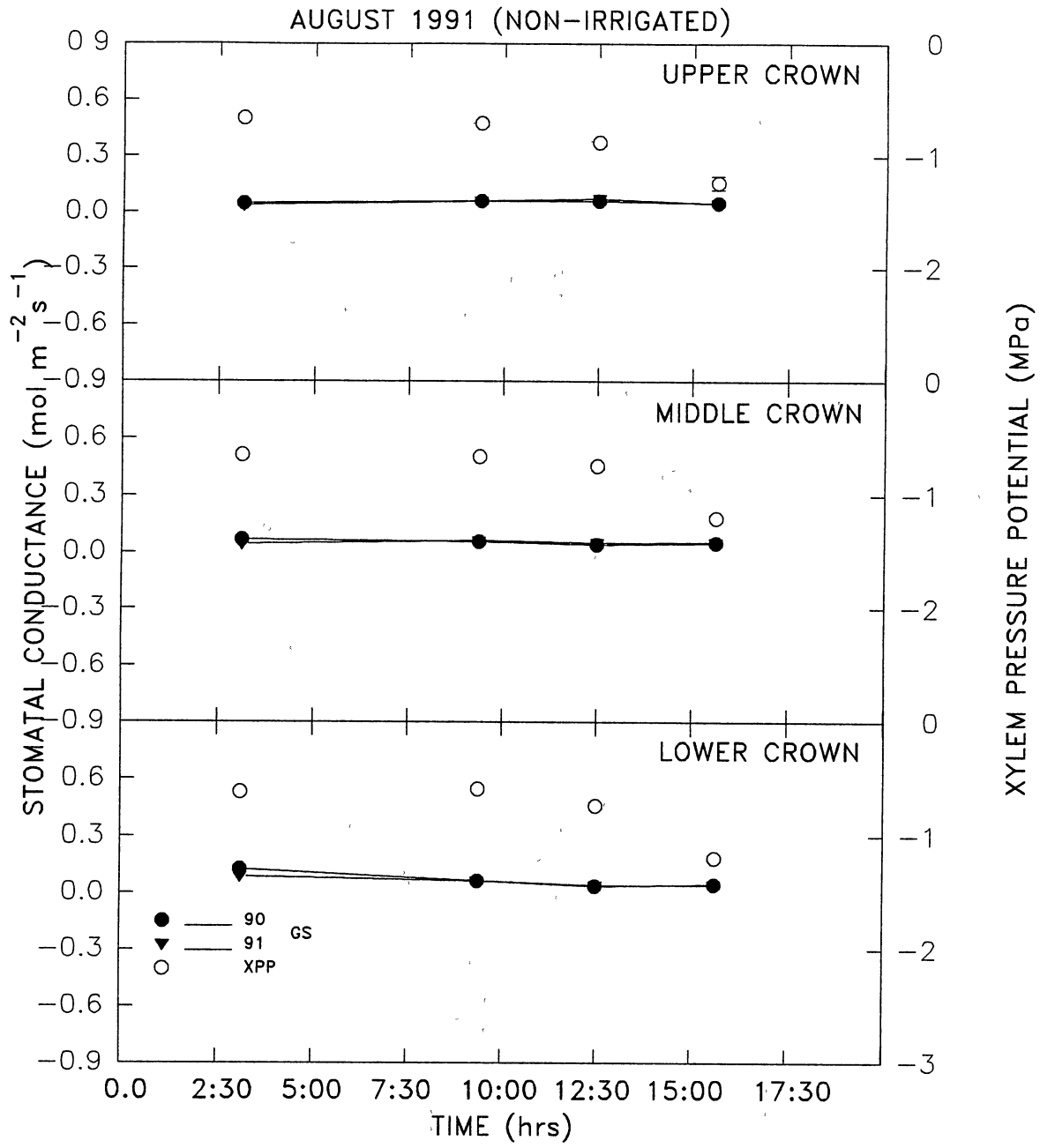

Figure 34. Diurnal patterns of stomatal conductance and xylem pressure potential for August. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

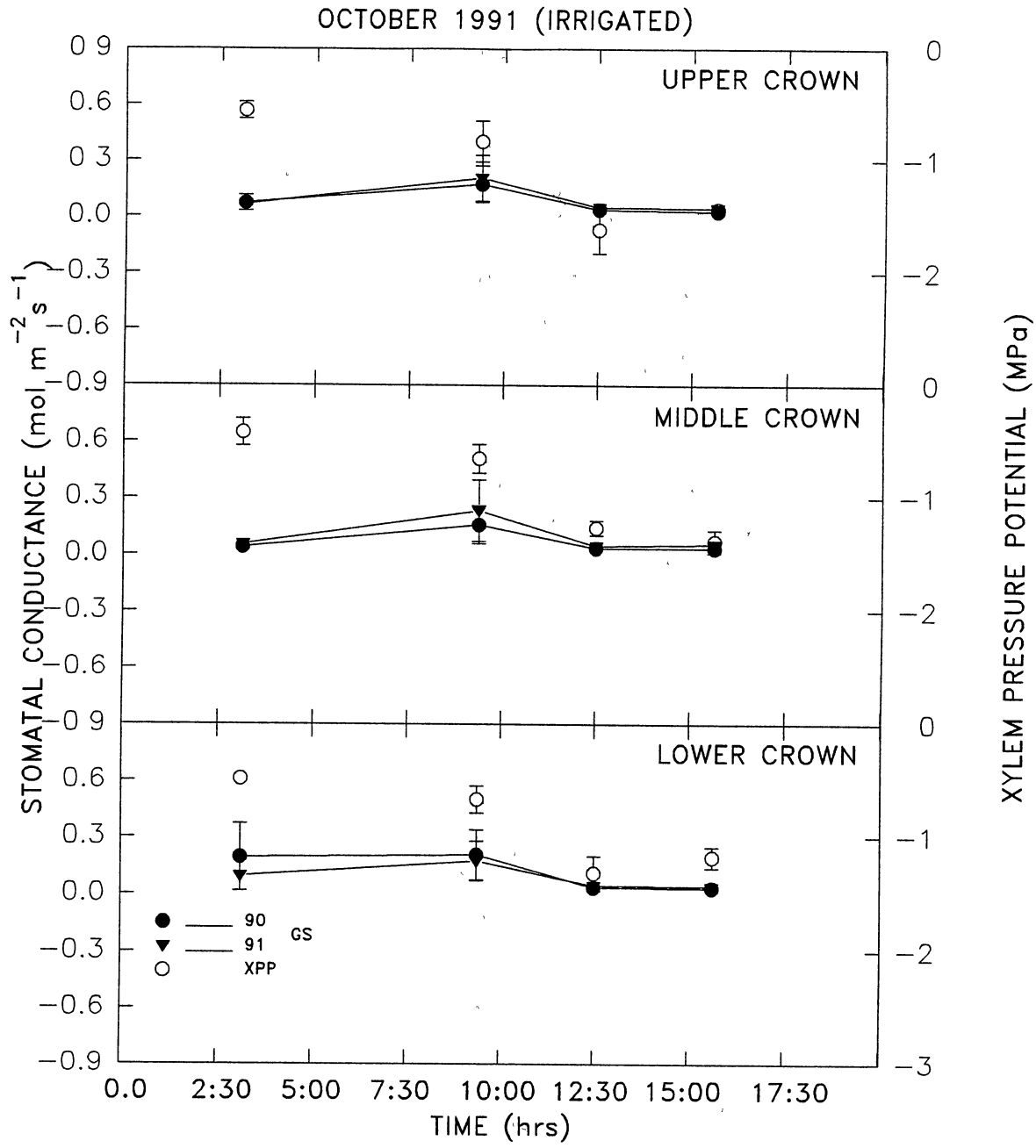

Figure 35. Diurnal patterns of stomatal conductance and xylem pressure potential for October. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

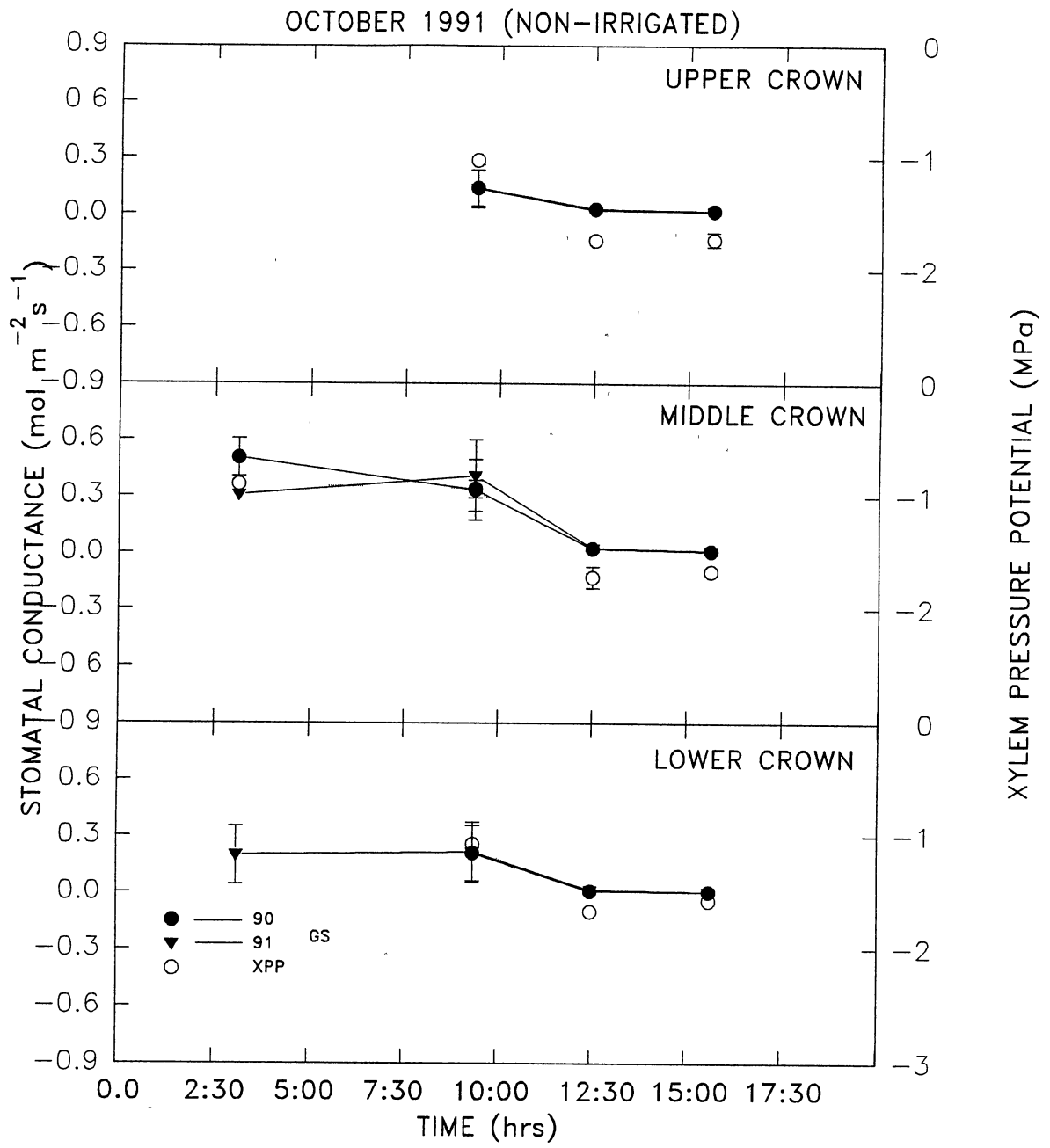

Figure 36. Diurnal patterns of stomatal conductance and xylem pressure potential for October. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

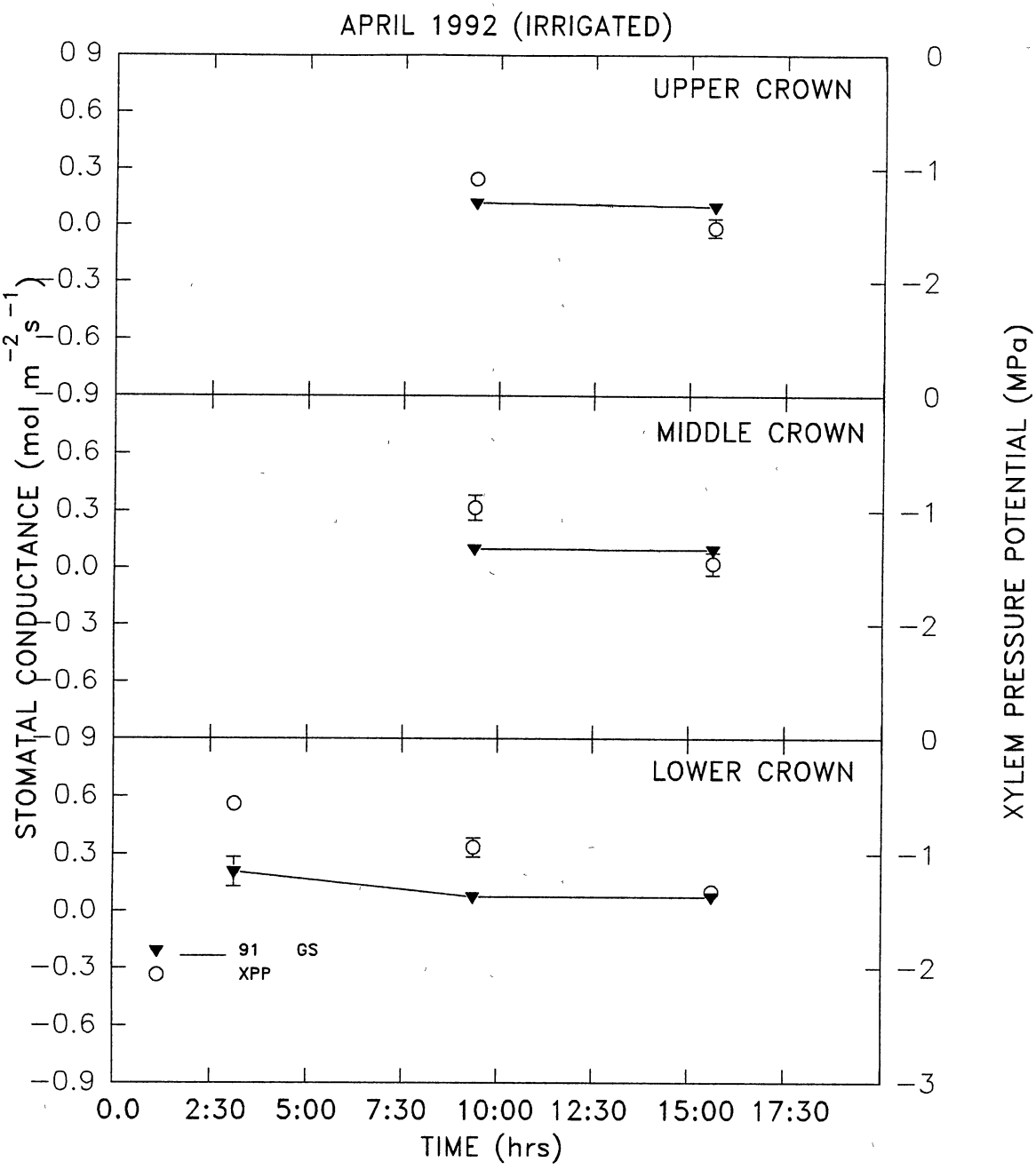

Figure 37. Diurnal patterns of stomatal conductance and xylem pressure potential for April. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

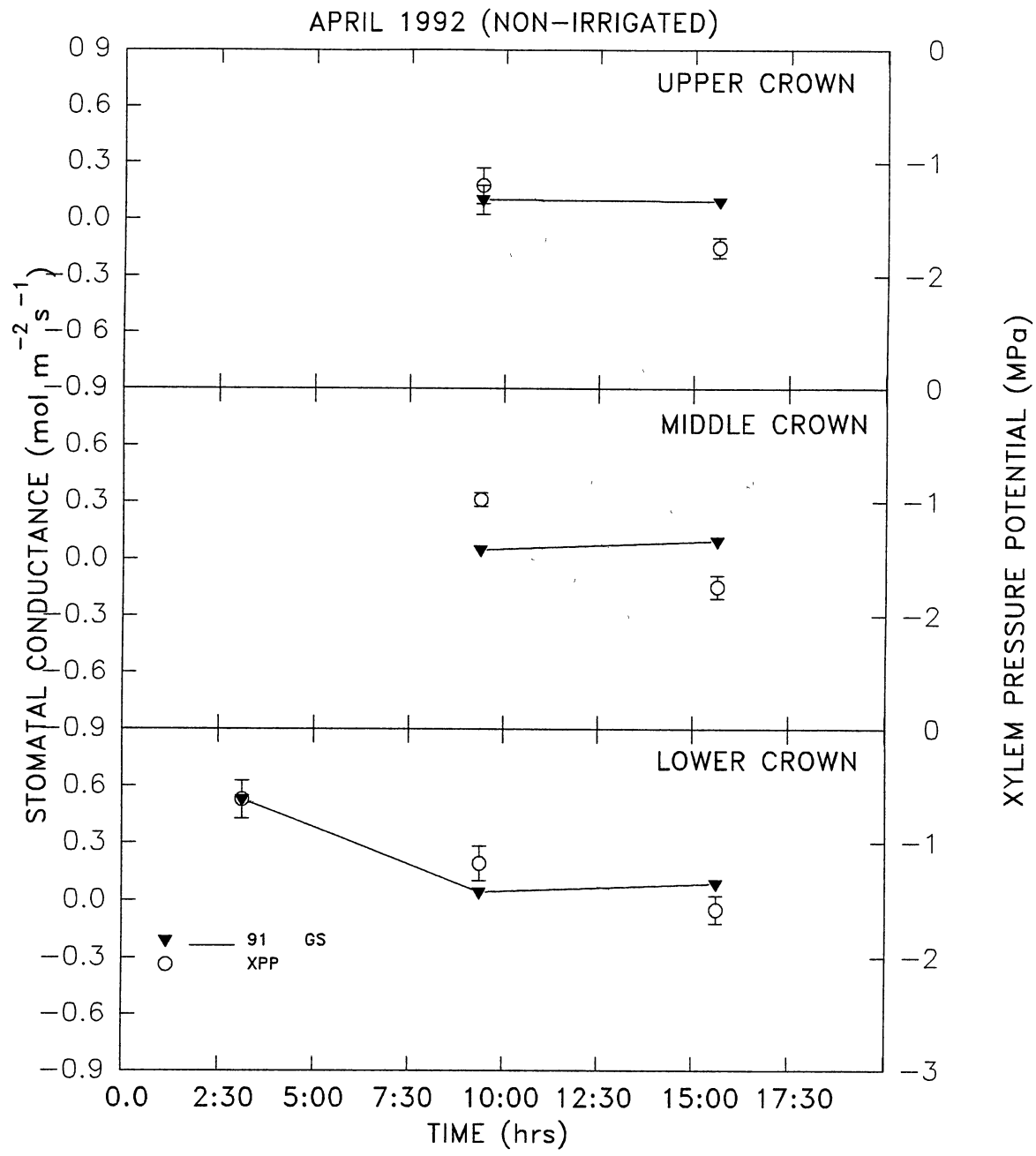

Figure 38. Diurnal patterns of stomatal conductance and xylem pressure potential for April. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

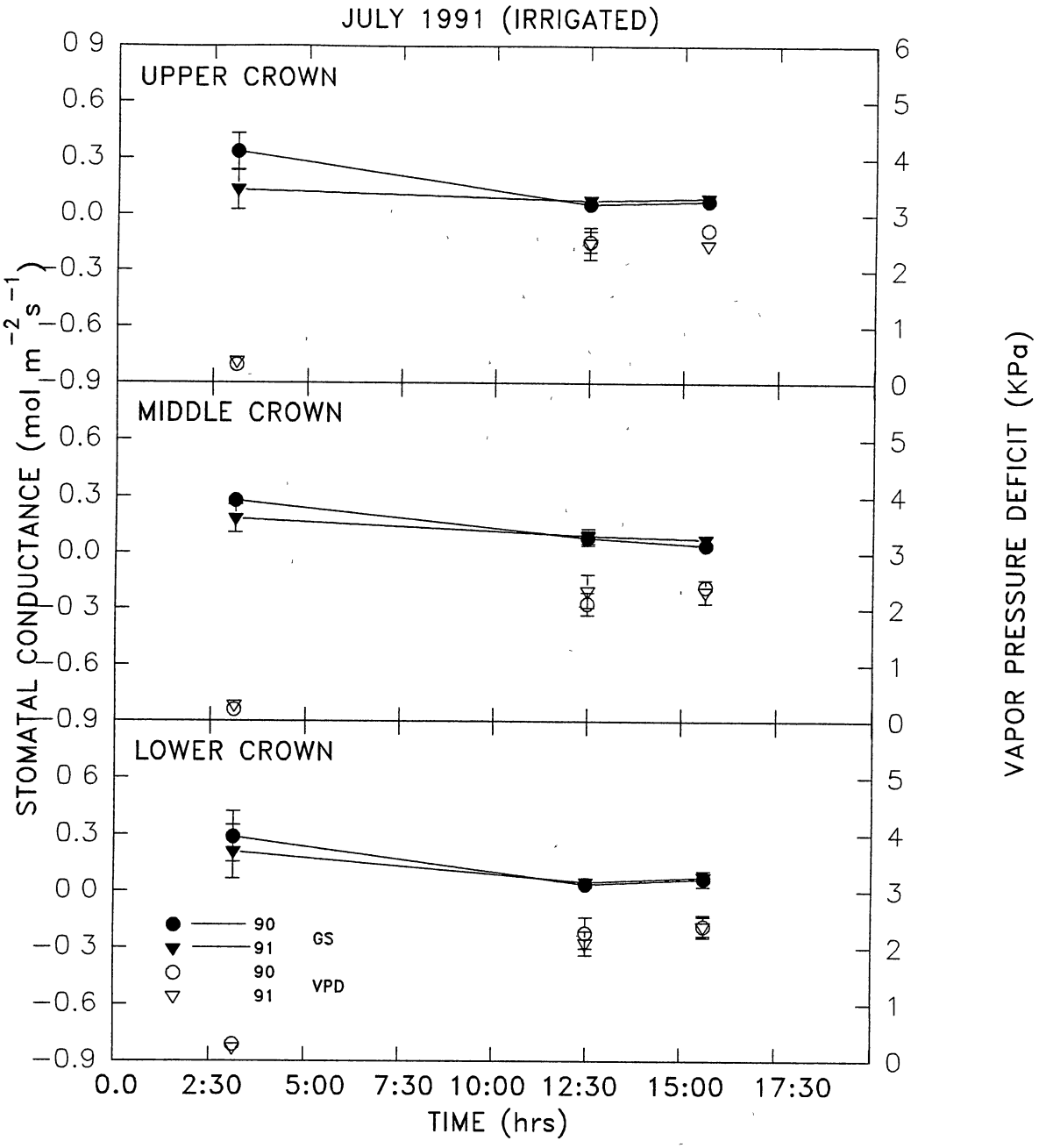

Figure 39. Diurnal patterns of stomatal conductance and vapor pressure deficit for July. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

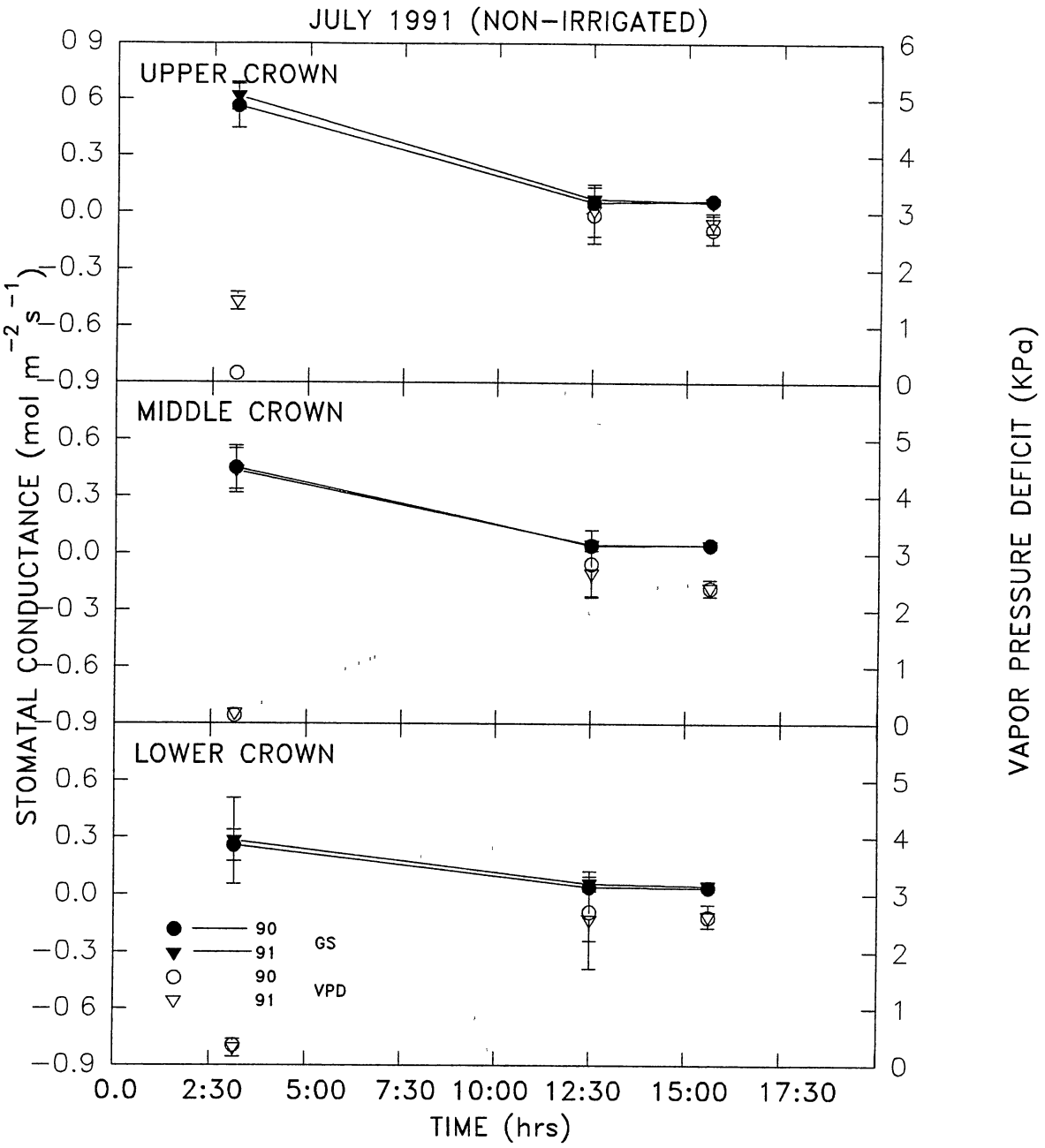

Figure 40. Diurnal patterns of stomatal conductance and vapor pressure deficit for July. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

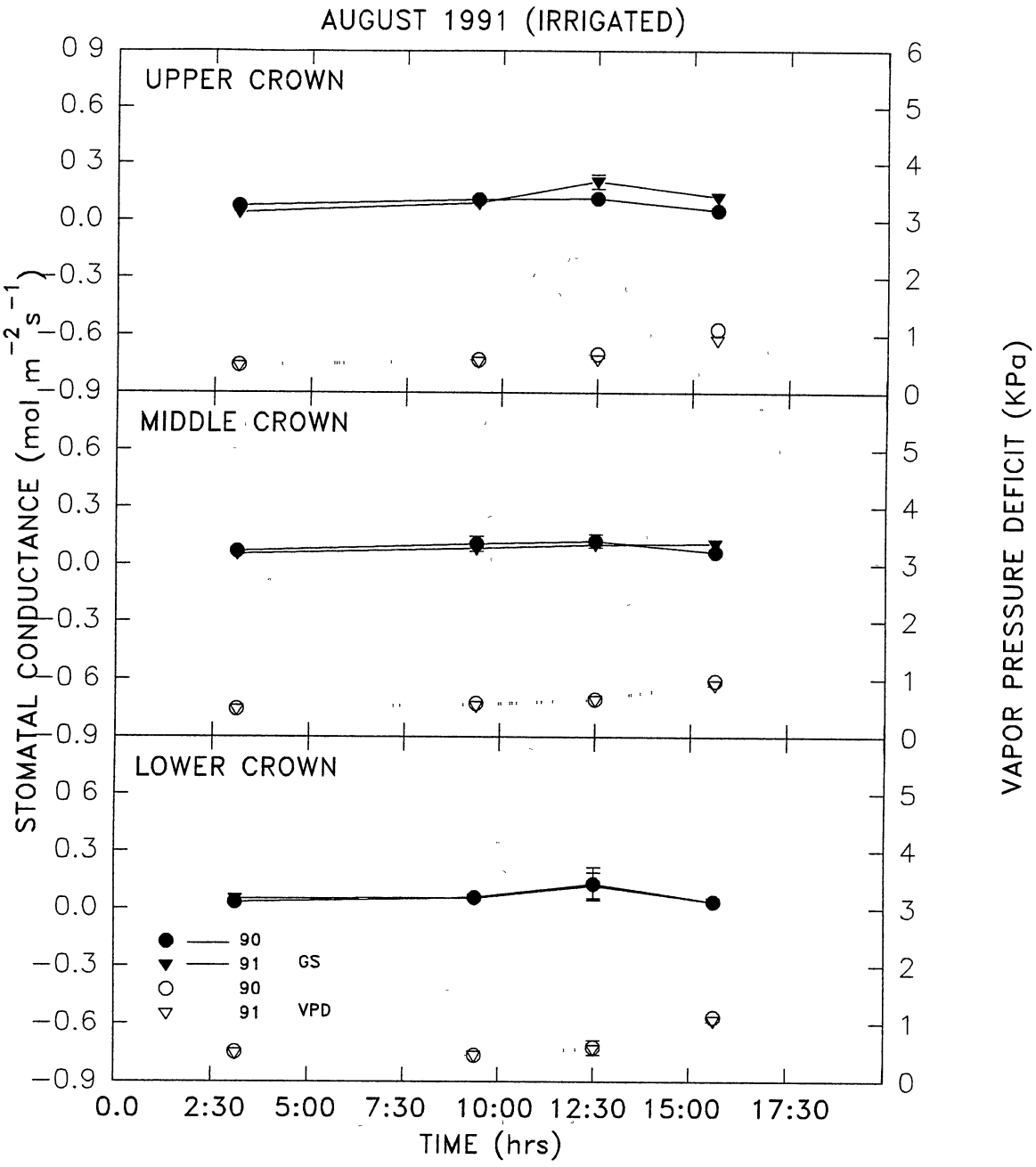

Figure 41. Diurnal patterns of stomatal conductance and vapor pressure deficit for August. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

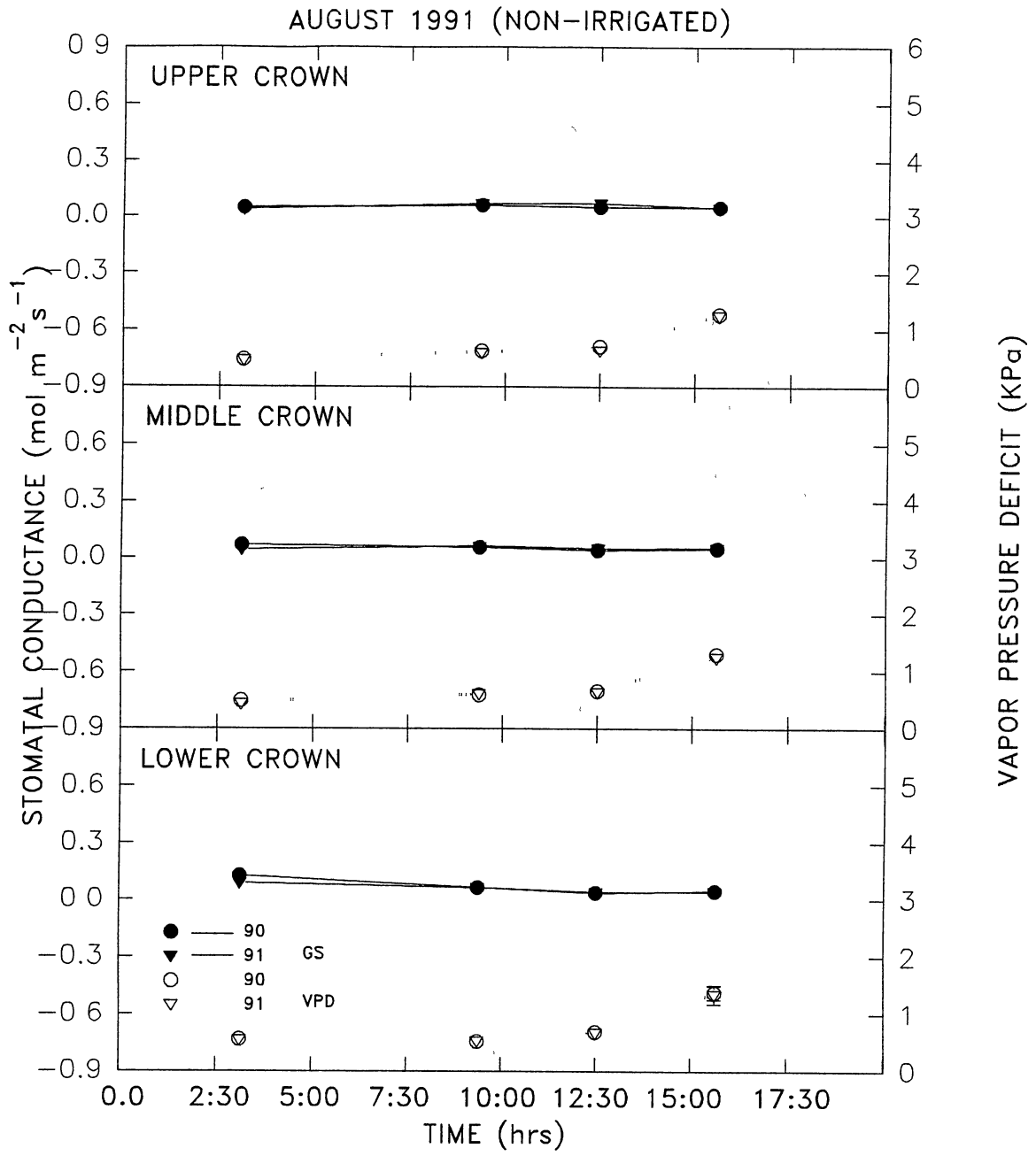

Figure 42. Diurnal patterns of stomatal conductance and vapor pressure deficit for August. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

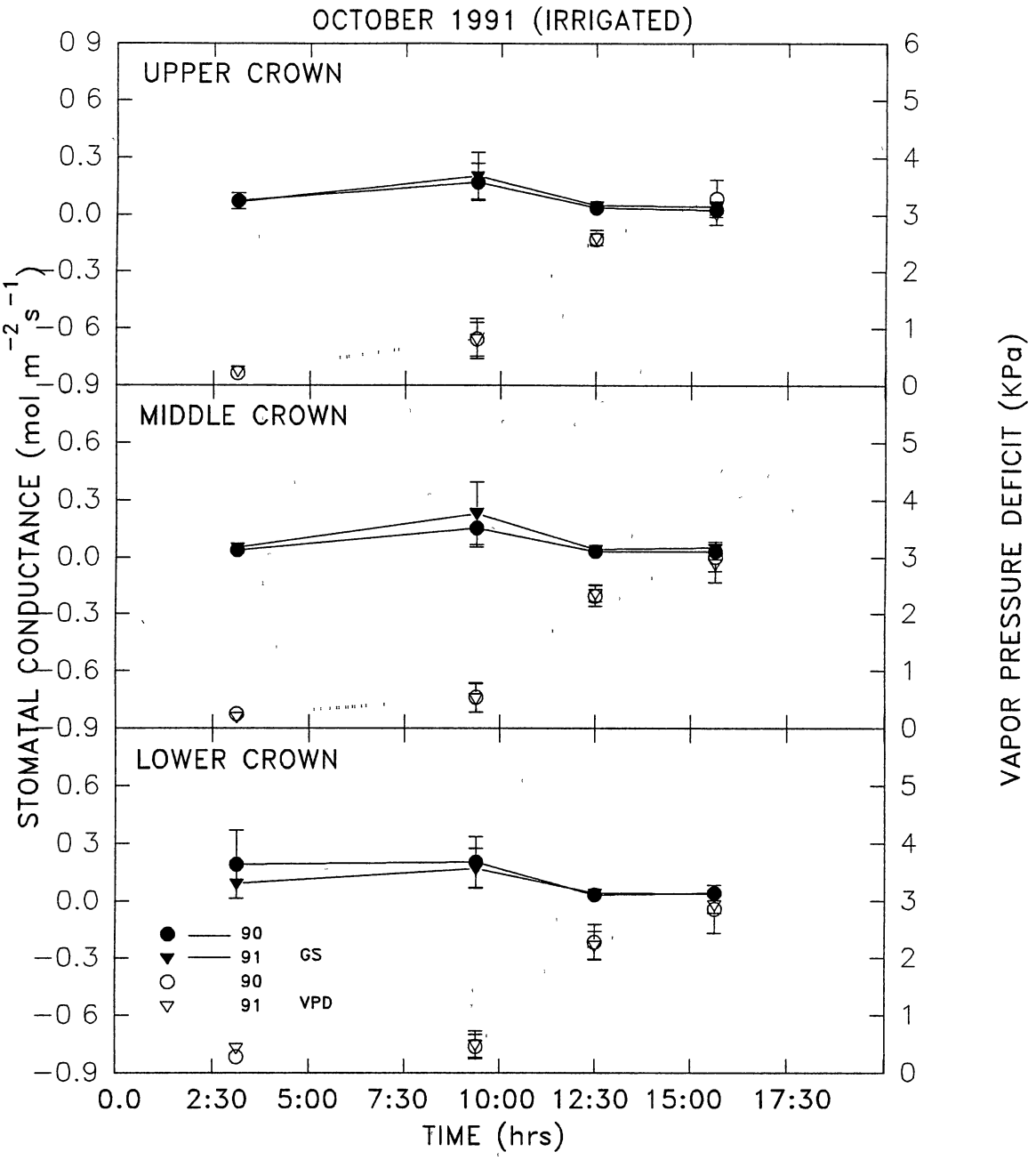

Figure 43. Diurnal patterns of stomatal conductance and vapor pressure deficit for October. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

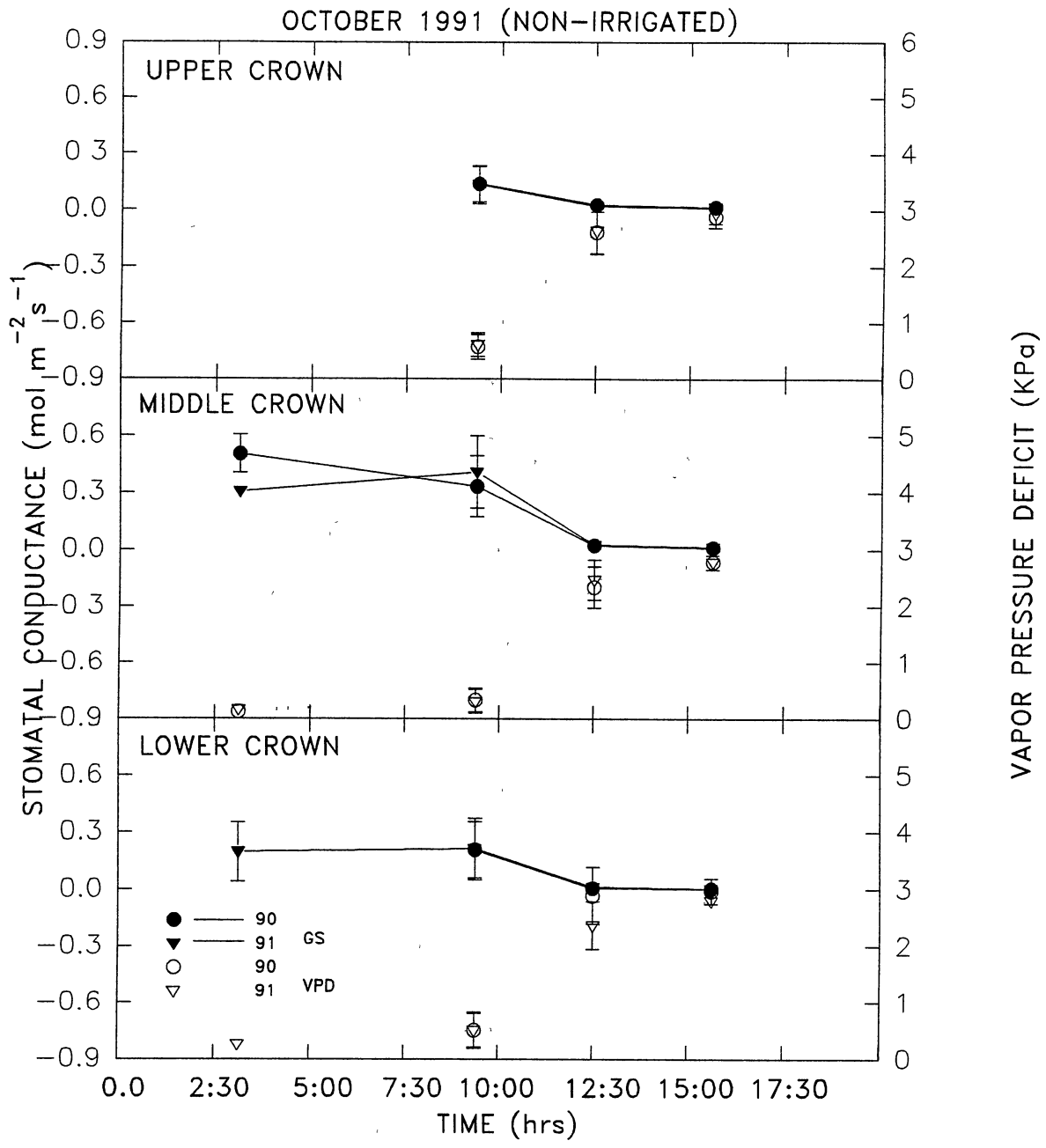

Figure 44. Diurnal patterns of stomatal conductance and vapor pressure deficit for October. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

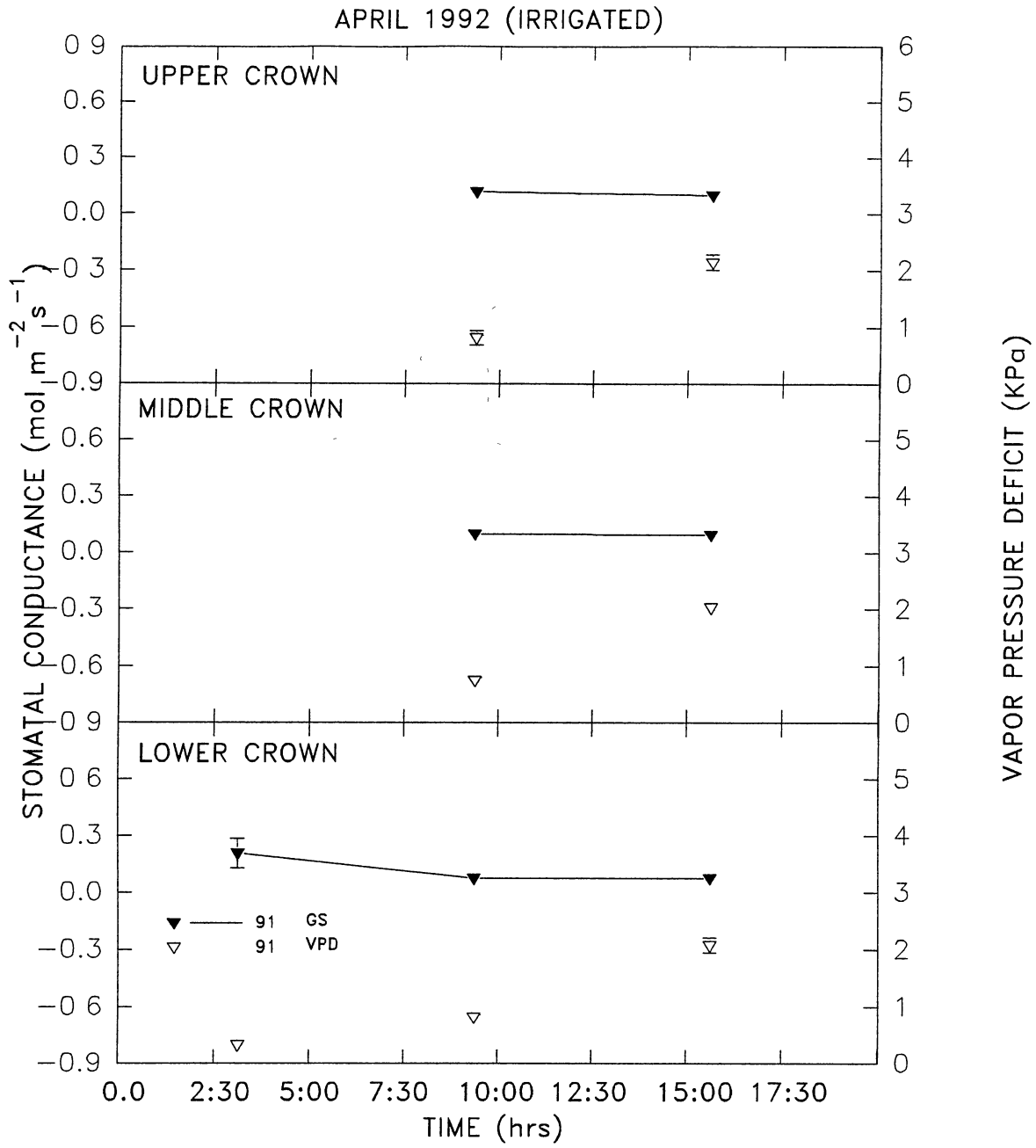

Figure 45. Diurnal patterns of stomatal conductance and vapor pressure deficit for April. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

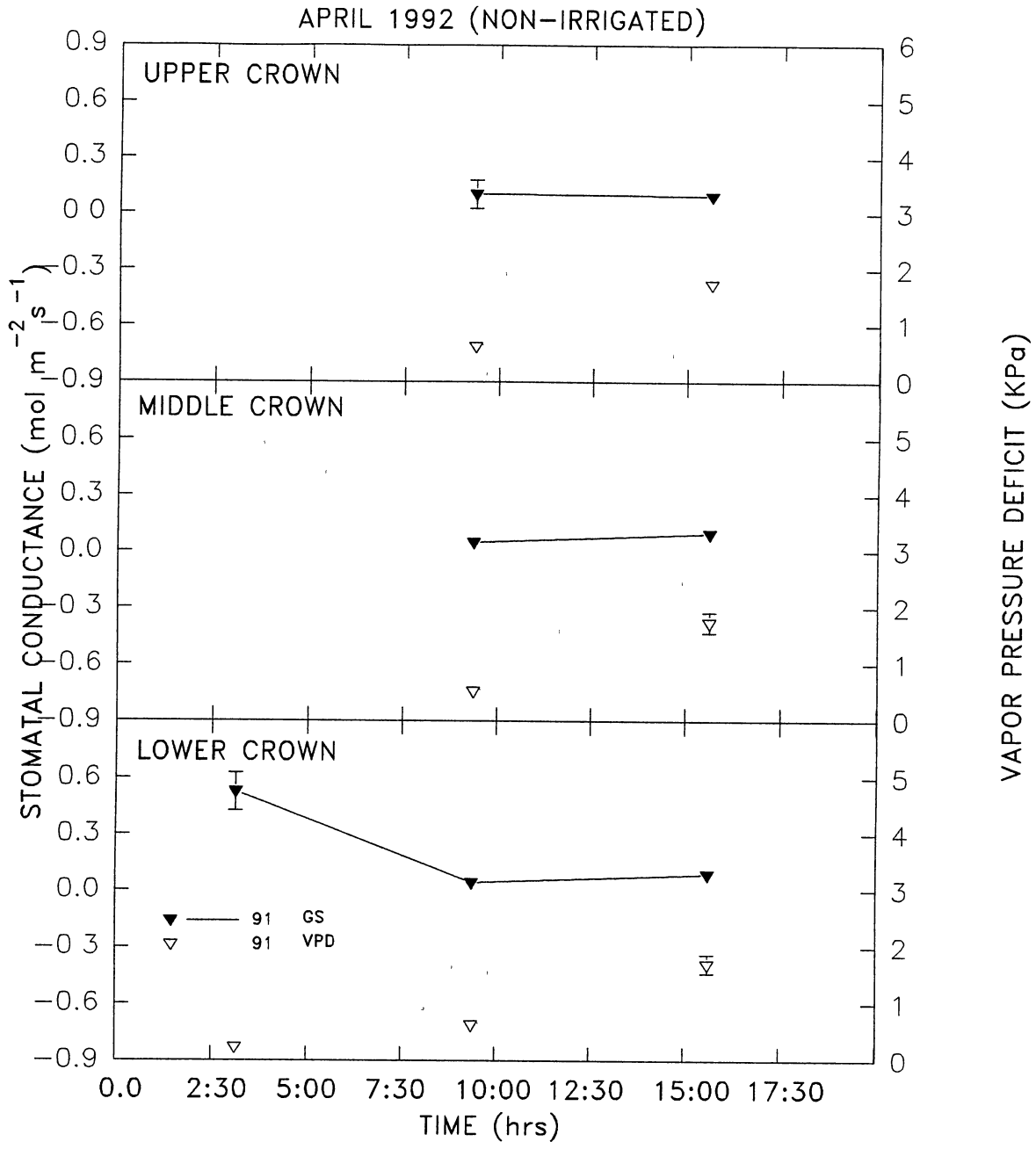

Figure 46. Diurnal patterns of stomatal conductance and vapor pressure deficit for April. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

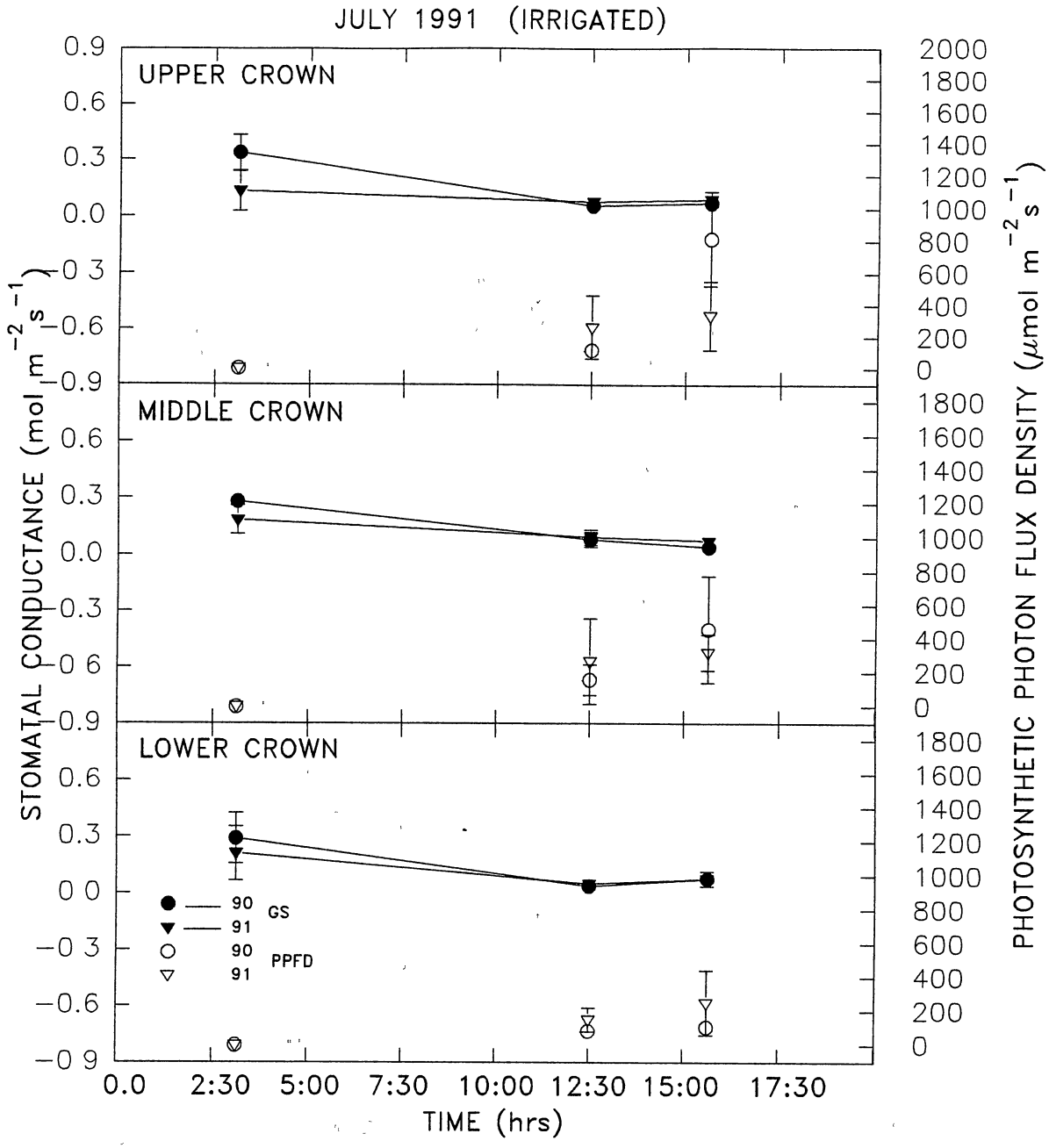

Figure 47. Diurnal patterns of stomatal conductance and photosynthetic photon flux density for July. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

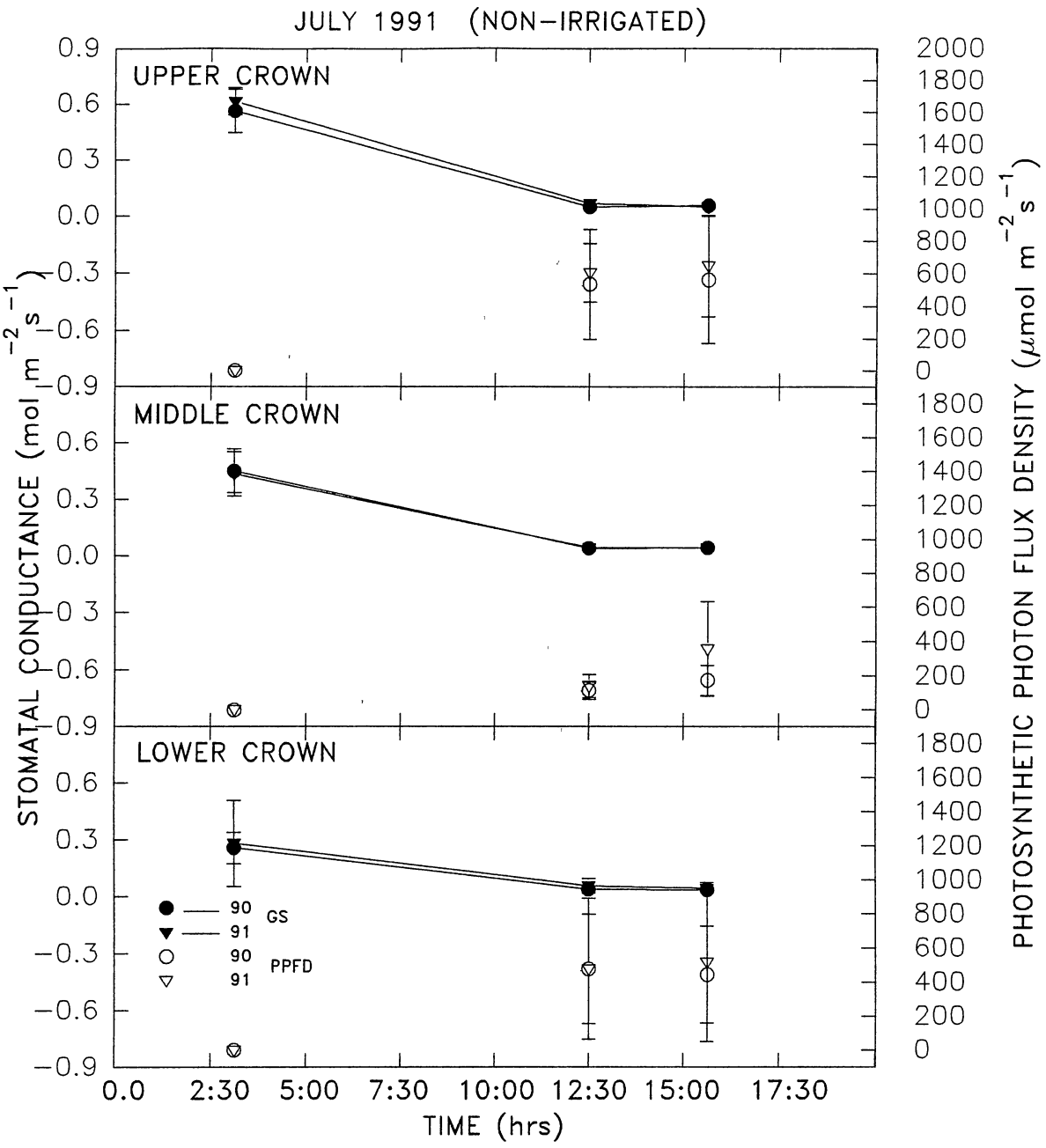

Figure 48. Diurnal patterns of stomatal conductance and photosynthetic photon flux density for July. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

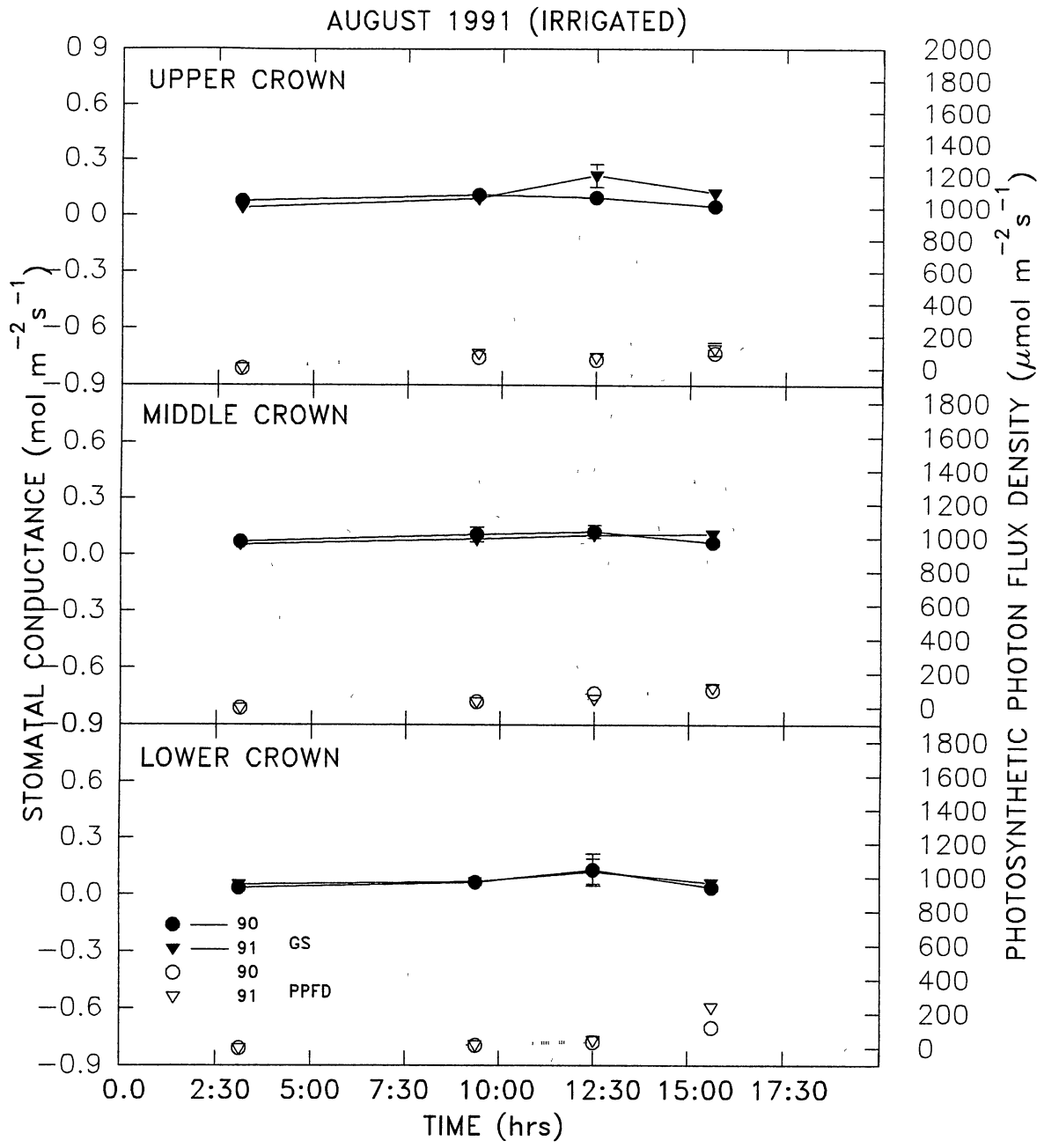

Figure 49. Diurnal patterns of stomatal conductance and photosynthetic photon flux density for August. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

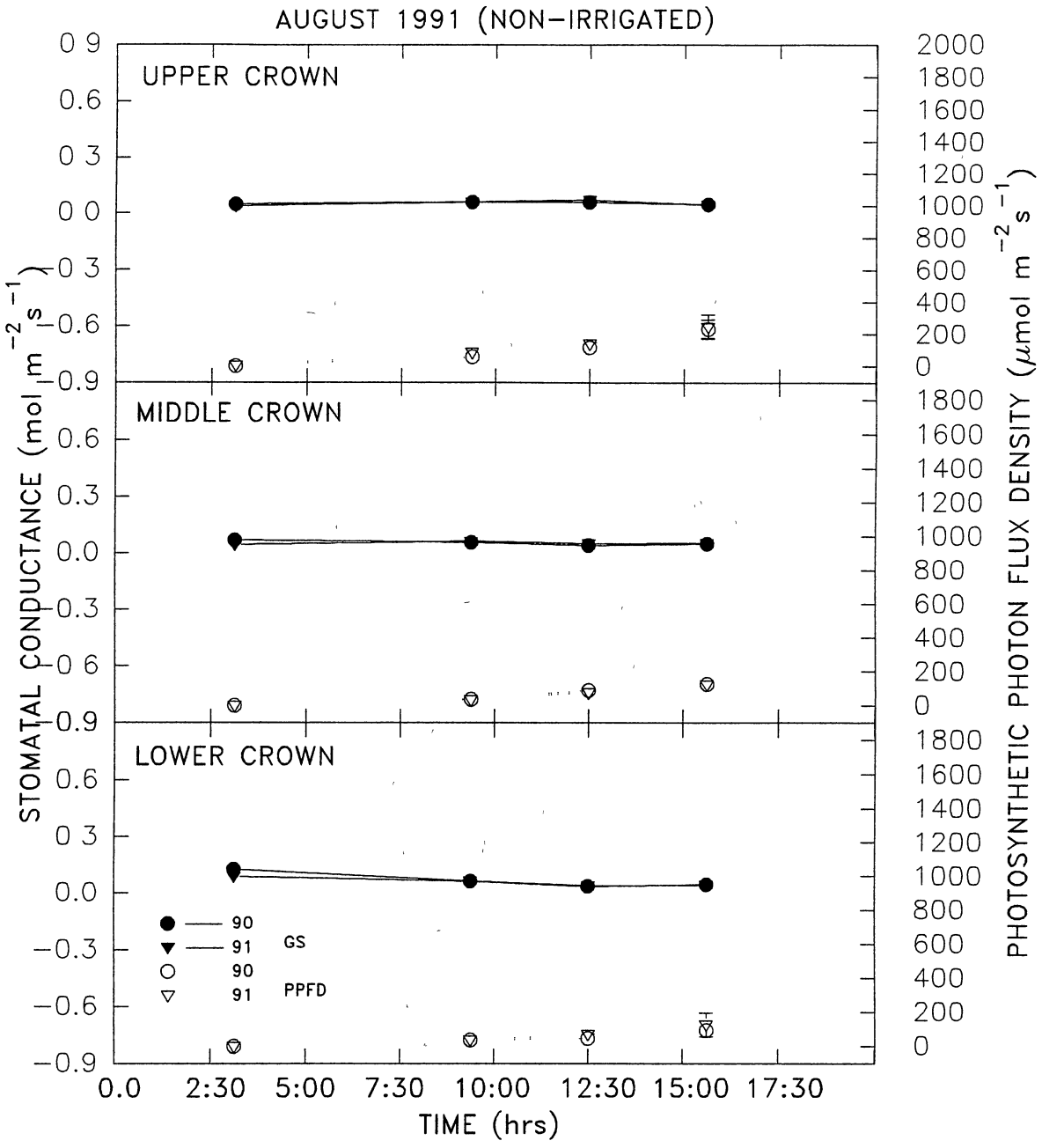

Figure 50. Diurnal patterns of stomatal conductance and photosynthetic photon flux density for August. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

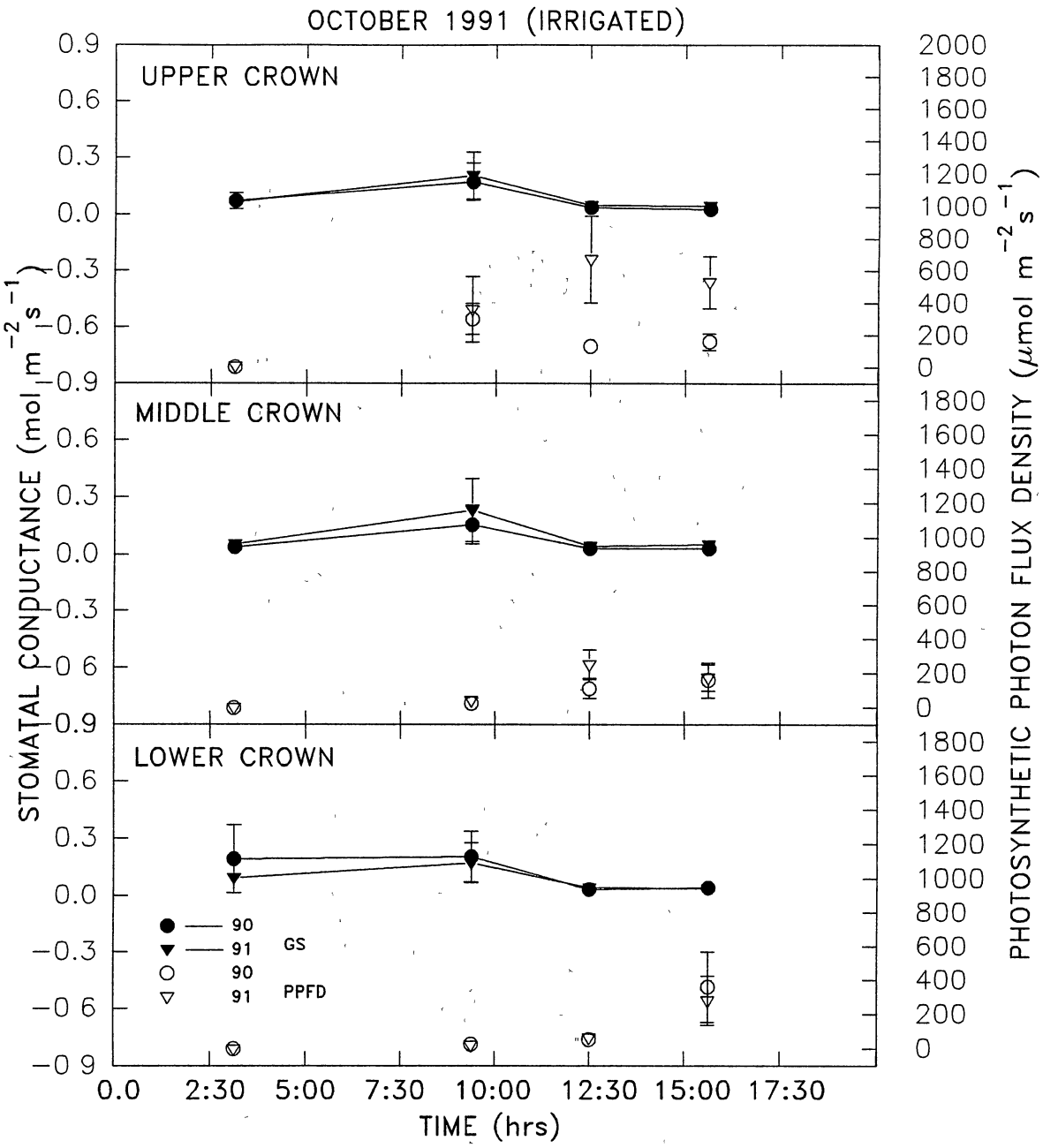

Figure 51. Diurnal patterns of stomatal conductance and photosynthetic photon flux density for October. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

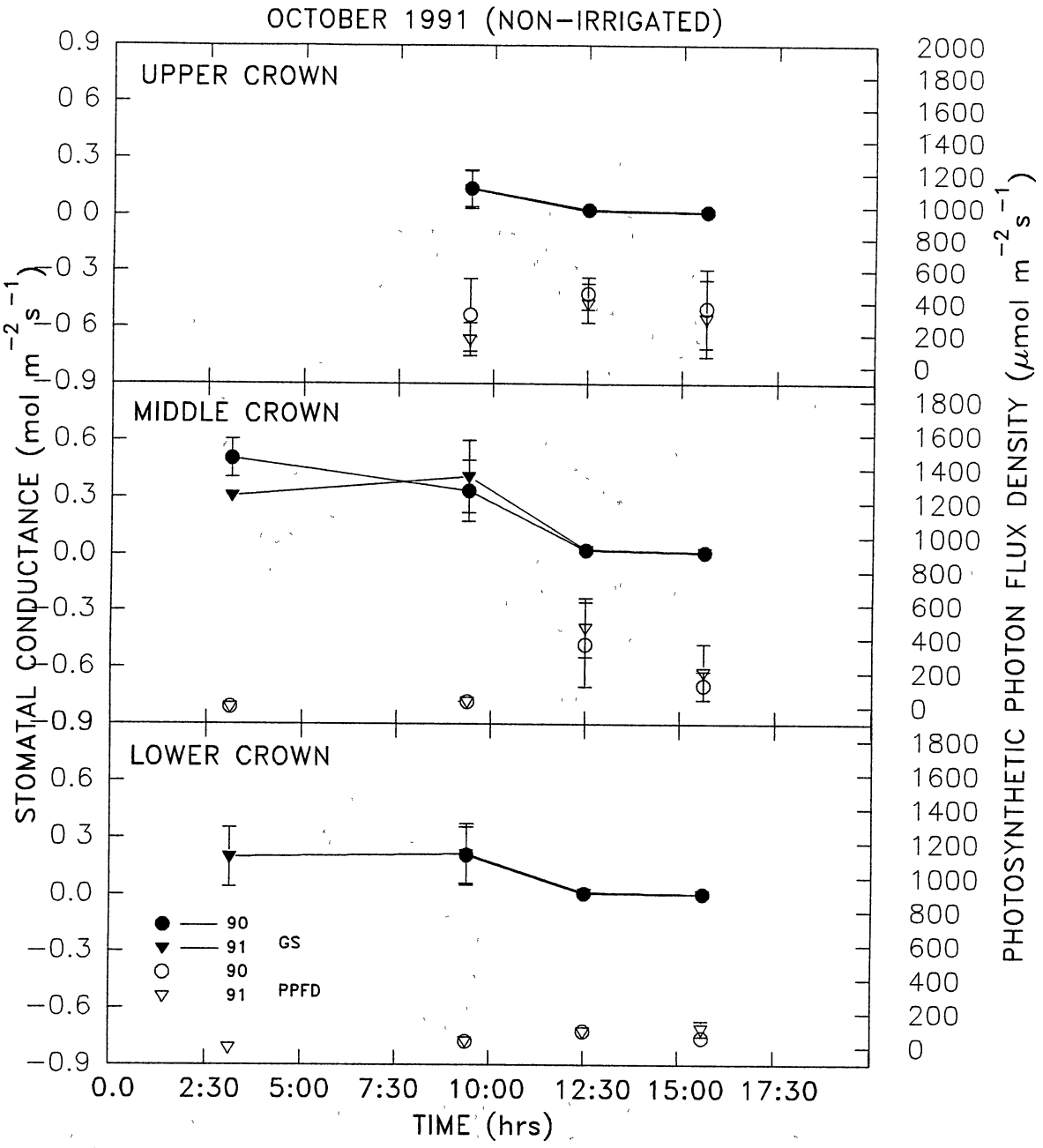

Figure 52. Diurnal patterns of stomatal conductance and photosynthetic photon flux density for October. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

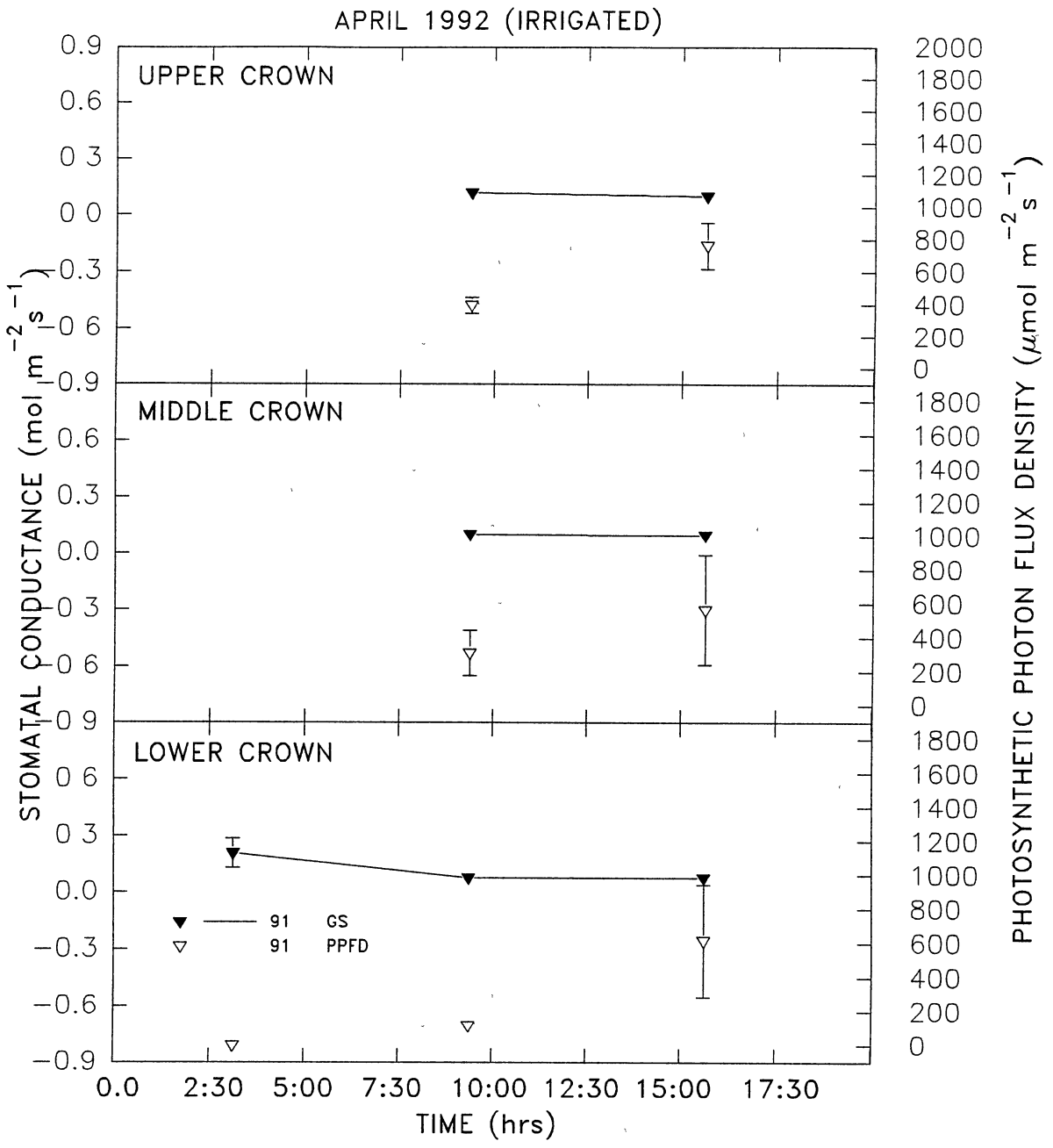

Figure 53. Diurnal patterns of stomatal conductance and photosynthetic photon flux density for April. Each bar indicates one standard error and each point indicates the mean of three trees measured in the irrigated plot.

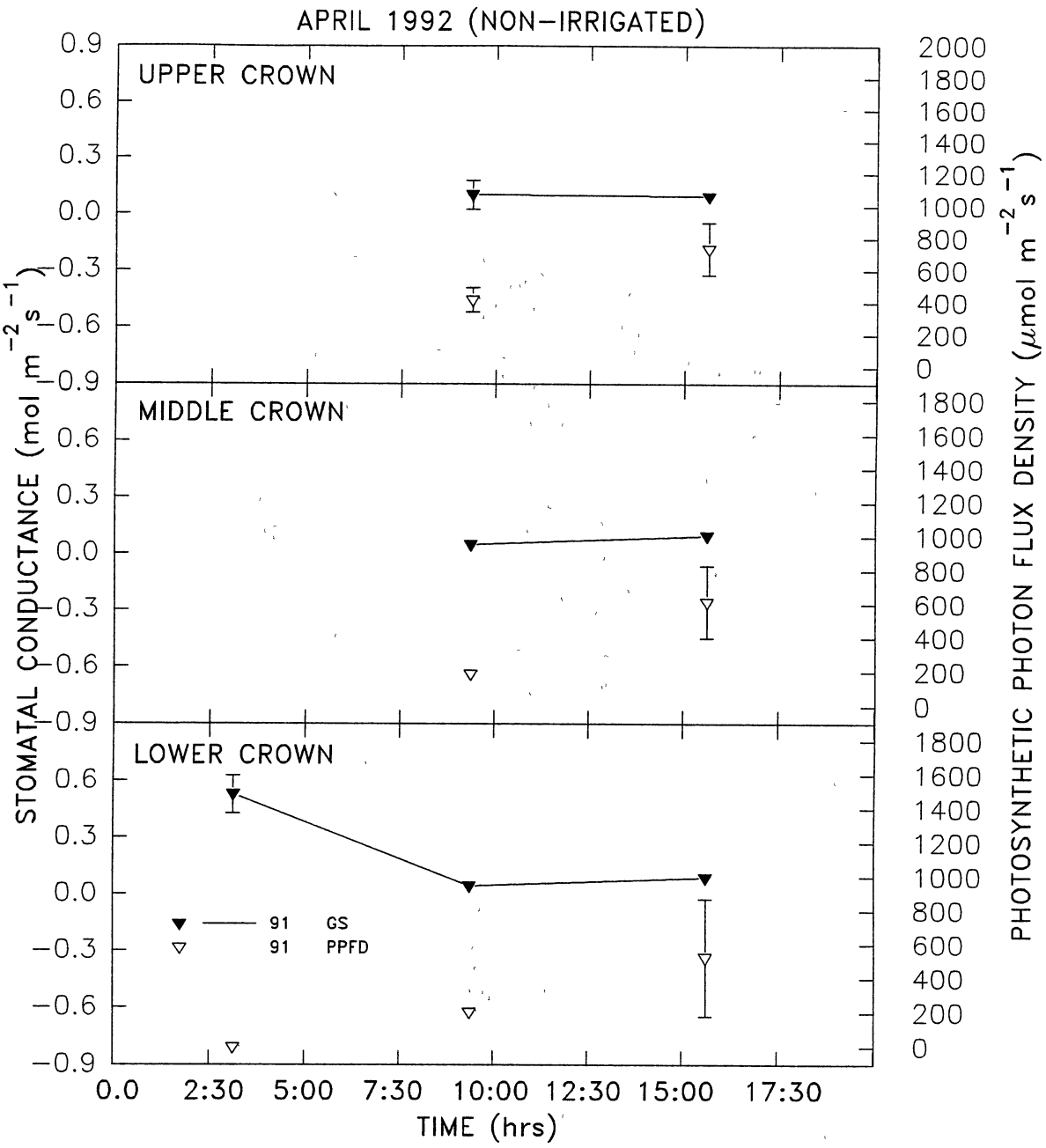

Figure 54. Diurnal patterns of stomatal conductance and photosynthetic photon flux density for April. Each bar indicates one standard error and each point indicates the mean of three trees measured in the non-irrigated plot.

VITA

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Candidate for the Degree of

Master of Science

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Major Field: Forest Resources

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